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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

A REVISION OF THE SPHENOPSID ORGAN GENUS, *LITOSTROBUS*

By

Robert W. Baxter

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A Revision of the Sphenopsid Organ genus, *Litostrobus*[1]

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Robert W. Baxter

ABSTRACT

A number of excellently preserved fragments of *Litostrobus* cones from coal balls of the Desmoinesian Stage, Middle Pennsylvanian of Iowa are described. Evidence is presented to show that a wide variation in number and arrangement of sporangia and bracts occurs in different whorls of individual cones with an apparent decrease in number towards the cone apex. Heteromorphism of 14 to 6 sporangia per whorl is accompanied by changes in the number and arrangement of the subtending bracts so that apical whorls of 6 sporangia may have double the number of alternate and opposite bracts while basal whorls of 14 sporangia may have only an equal number of alternate bracts. The vascular system is shown to be simple as originally described by Mamay (1954) rather than the triple dichotomy described by Reed (1956). The cone of *Mesidiophyton* Leisman is shown to be congeneric with *Litostrobus* but to constitute a distinct species, *L. paulus*. New diagnoses are given for both *L. iowensis* and *L. paulus*. Possible relationships of *Sphenostrobus* to *Litostrobus* are discussed.

INTRODUCTION

The organ genus *Litostrobus* was established by Mamay (1954) on a single specimen of a sphenopsid cone found in a coal ball from the Urbandale Coal Mine, Urbandale, Iowa. The stratigraphic position of the type species, *L. iowensis,* is Desmoinesian Stage, Middle Pennsylvanian. The generic diagnosis was given as follows: "Cone verticillate, the appendages produced in multiples of three. Whorls superposed, each consisting of ba-

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[1] This is part of a general investigation of the Pennsylvanian Coal ball flora supported by National Science Foundation grant GB 4933.

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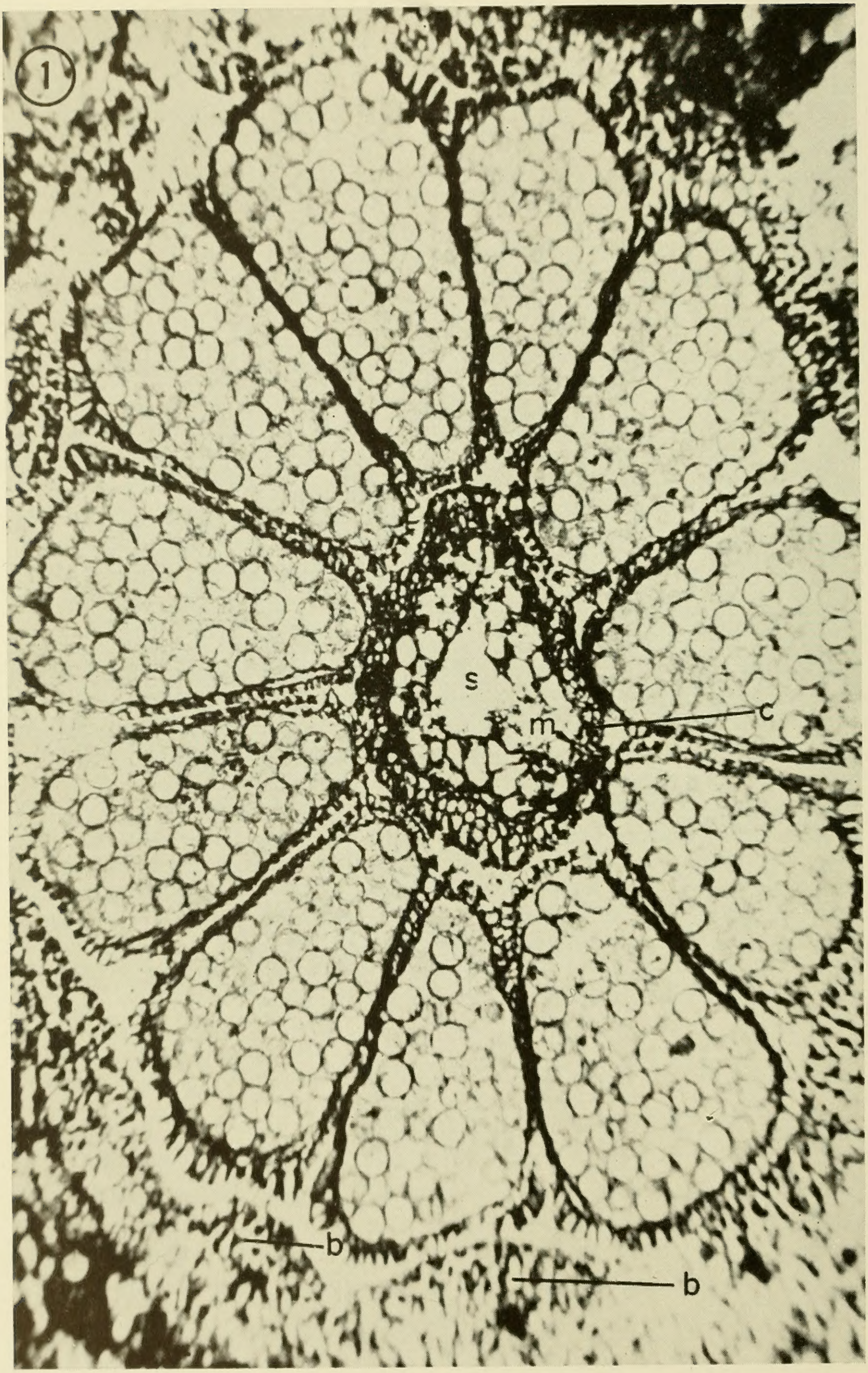
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sally fused bracts and axillary sporangia. Bracts twice as numerous as sporangia, arranged one opposite a sporangium, one alternate. Sporangia orthotropus, each terminating a short axillary pedicel."

Additional specimens from the Weir-Pittsburg Coal of Frontenac, Kansas were described and placed in the same genus and species as Mamay's material by Reed (1956) who also emended the generic diagnosis to include an elaborate triple dichotomy of the vascular traces into the bracts and axillary sporangiophores.

The present account is concerned with the description of a number of exceptionally well preserved cones discovered in a coal ball from the Mich Mine of Oskaloosa, Iowa, of the same stratigraphic position as the Urbandale Mine. These cones are clearly assignable to the genus *Litostrobus*, but they show a number of variations from both Mamay's and Reed's specimens which make it necessary to further revise the original concept of the cone structure.

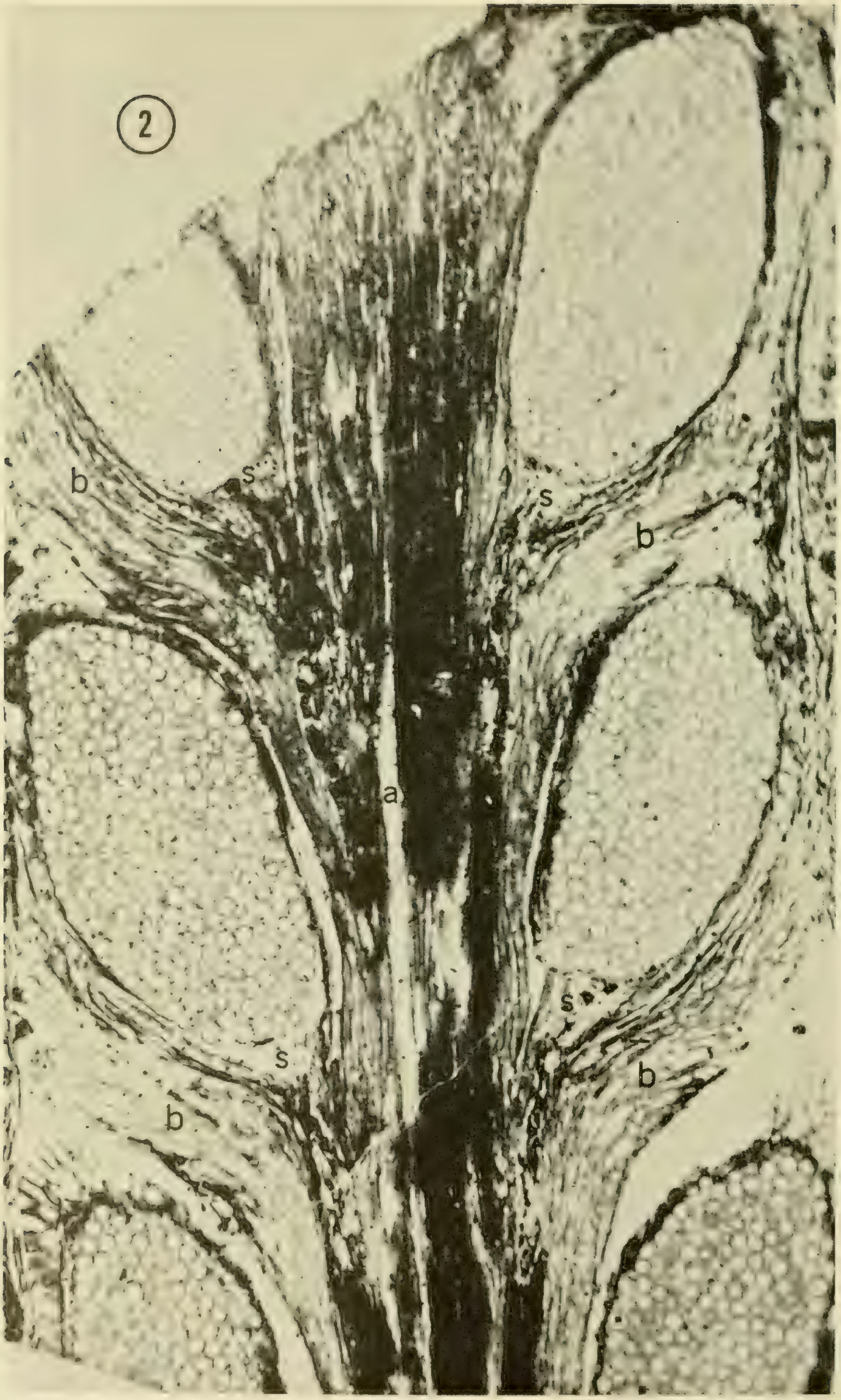
DESCRIPTION

Nine different fragments of cones were exposed in one coal ball and one in another. Whether they all represented different cones or fragments of a few cones is uncertain, but as the longest specimen exposed reached 25 mm with no sign of tapering at either end, it may be assumed that a number of the transverse exposures probably represented the curving path of single long cones. All of the specimens were close to 4.0 mm in diameter.

Three of the specimens were cut in the longitudinal plane which permitted several complete series of tangential and radial sections, while the other 7 specimens were worked out by extensive series of transverse sections. All of the specimens appear to be identical to the type species described by Mamay except for variations in the number and arrangement of sporangia and bracts per whorl. Since these variations were observed within a single cone, they are obviously of minor taxonomic significance. The present specimens do, however, show exceptionally fine preservation of almost all the tissues and accordingly supply a number of new details regarding the general cone anatomy which have been unavailable previously.

THE AXIS: A very small triarch, exarch, protostele only 320 μ from one protoxylem point to another occupies the exact center of the cone axis. The protoxylem is situated at the three corners of the triangle and consists of small tracheids with spiral and annular thickenings while the larger, thin walled metaxylem tracheids show multiseriate bordered pits (Fig. 24) with the narrow opposing appertures forming an X-shaped pattern in the center

FIG. 1. *Litostrobus iowensis.* Transverse section of cone with 11 sporangia per whorl. The central triangular area in the axis is occupied by the triarch protostele(s) (here missing) and is surrounded by the large cells of the melasmatic zone (M) which is enclosed by the smaller celled cortex (C). The 11 sporangia are enclosed by the ascending bracts (b). X30.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of the border. The pits are very small with the diameter of the entire border averaging only 8 μ. No secondary xylem is present in any specimen.

While the general character of the triarch protostele and the pitting of the tracheids is typically sphenophyllalean, it is distinctive in its extemely small size (compared to known species of other sphenophyllalean cones) and the very fragile, thin-walled nature of the tracheids—particularly those of the metaxylem. These seem to be so consistently delicate that, in spite of generally excellent preservation of all other tissues, the area of the stele is usually only evident as a triangular open area in the center of the axis. (Figs. 1, 2, 14, 15).

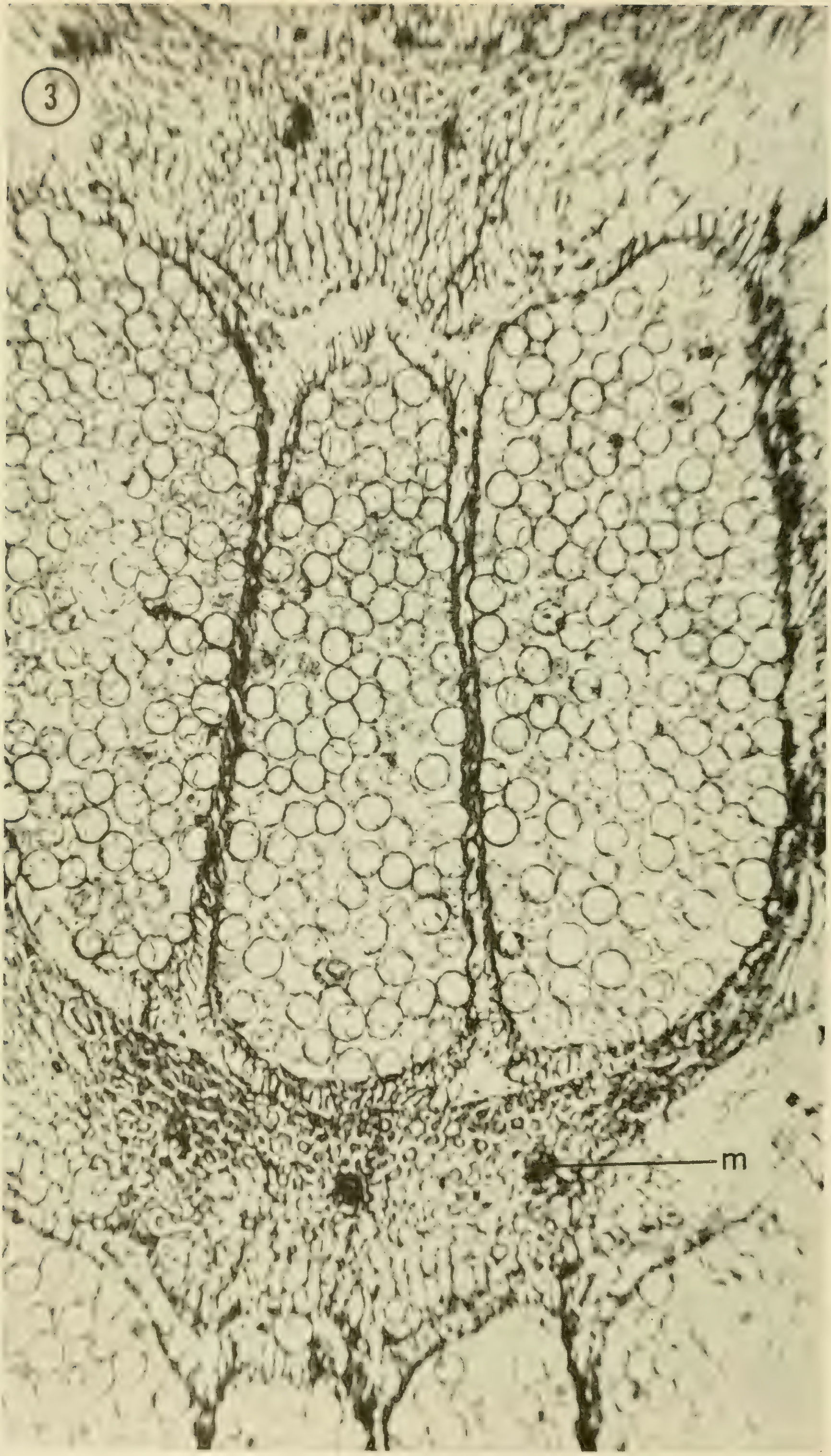
The triangular stelar area is immediately surrounded by a conspicuous zone of large cells, tubular in character, reaching 1.5 mm in length and 90 μ in diameter. The zone is usually 2-4 cells thick with each cell filled with an opaque "resin". The cells and their contents are similar to the tissue described by Leisman (1964) for the cone of *Mesidiophyton paulus* for which he used the term "melasmatic," a term which also seems appropriate in this case. These "melasmatic" cells have been described previously in other sphenopsid organ genera such as *Asterophyllitis charaeformis* (Thomas, 1911), in *Sphenostrobus thompsonii* (Levittan and Barghoorn, 1948), and *Calamostachys americana* (Arnold, 1958).

Directly outside of the melasmatic zone is the axis cortex consisting of 2-4 layers of cells with a vertical length up of 270 μ and an average transverse dimension of 40 x 65 μ with the radial width the greater. These cells have thin, smooth walls and are always devoid of contents (Figs. 1, 15).

THE BRACTS: The bracts of each whorl are fused internally to form a broad, cup shaped receptacle enclosing the axillary sporangiophores and sporangia. They consist of the same cell type making up the cortex of the axis which becomes gradually thicker in the upper part of the lower internode and then flares out at the node at about a 45° angle to form the bract disc (Fig. 2). In the mature, central part of the cones the bracts average 3.7 mm in length and extend about one half the way into the next internode above. The individual bracts do not separate until a point about 0.8-1.0 mm above the base of the disc so that the axillary sporangiophores and lower part of the sporangia are completely enclosed (Fig. 14).

At the level of separation from the disc, the bracts are fusiform in transverse outline and are 1.0 mm in tangential width at their broadest point (Fig. 23). The central area of each bract is traversed by a conspicuous strand of melasmatic cells, continuous with the melasmatic zone of the cone axis (Fig. 3), which it is felt has been misidentified as the vascular trace in most previous specimens. The true vascular trace is adaxial to the melasmatic strand and consists of never more than 2-3 very small tracheids about 6-8 μ in

FIG. 2. *Litostrobus iowensis*. Median-longitudinal (radial) section of cone. S, sporangiophore; b, bract; a, central area of axis stele. Note superposed position of sporangiophores and elongate sporangia packed with spores. X25.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diameter with spiral and annular thickenings. These traces are so small that only in a very few cases of exceptionally good preservation was it possible to see them at all. However, all of the evidence points to the impression that the trace enters the bract directly from the protoxylem area of the axis stele without any intermediate branching.

The number of bracts, per whorl, varies from as few as 8 to more than 14 and their relation to the sporangia was equally variable being usually alternate but occasionally also in an opposite position. The significance of this variability is covered more fully in the discussion.

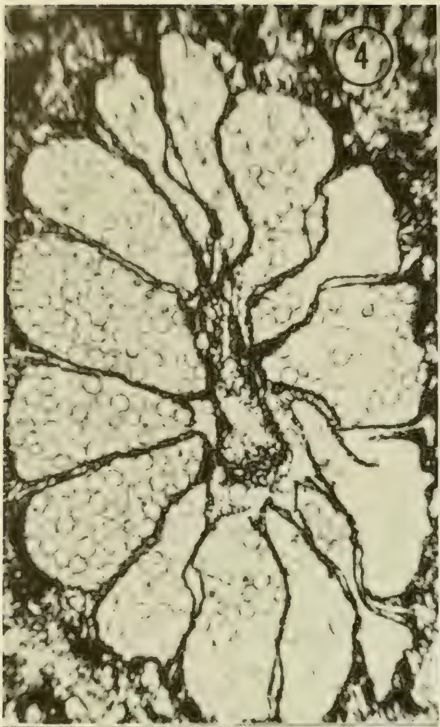
The sporangiophores and sporangia: The sporangiophores, or pedicels, arise in the axil of the cone axis and the fused bracts. They average 0.5 to 0.7 mm in length with a radial width of 0.2 mm at the base to 0.4 mm at their apex (Figs. 2, 12). Their tissues consist of elongated, thin-walled cells similar to those of the outer cortex of the axis, traversed on the abaxial side by a strand of 4-6 tubular cells of the melasmatic tissue and on the adaxial side by a vascular trace (Figs. 14, 15). The vascular trace follows a direct, ascending path from the exarch protoxylem strands of the axis stele up to the base of the sporangium. There is no evidence, whatsoever, for the complex triple dichotomy of a common bract and sporangiophore trace such as described by Reed (1956). The sporangiophore trace is slender at its base but widens out at its apex (where it comes directly in contact with the sporangium wall) into an expanded wedge some 8-10 cells across in which the tracheids become relatively much broader and shorter than in lower regions (Figs. 12, 13).

Each sporangiophore bears a single, erect (orthotropous) sporangium. The sporangia are elongate with average dimensions of 2.4 mm in length to 1.2 x 0.8 mm in diameter, the radial width the greater (Figs. 1, 2, 10). The total length of 3.0 mm for the erect sporangia on their sporangiophores is such that the tips of the sporangia of one whorl extend well above the base of the bract disc of the next whorl above (Figs. 2, 7, 22). Accordingly, the general configuration of the cone (based on our 10 specimens) is like Mamay's (1954) Fig. 2 rather than Reed's (1956) Fig. 30 where the sporangia are described and illustrated as "sub-globose."

The outer sporangium wall consists of cells elongated in the plane of the sporangium length with average measurements of 230 μ long by 90 x 45 μ wide with the radial width being the larger. The cell walls are smooth and straight in outline and lack the inwardly projecting buttresses found in many calamitean cones.

An inner sporangial wall of several layers of "delicate, parenchymatous cells" was described by Mamay but is only rarely present in our material. The

Fig. 3. *Litostrobus iowensis.* Tangential section of cone showing disc of fused bracts at top and bottom with whorl of sprangia above lower disc. M, melasmatic strands in bract disc. X50.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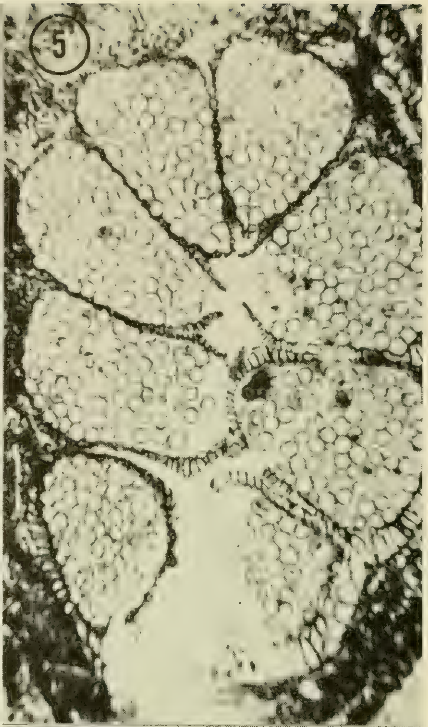
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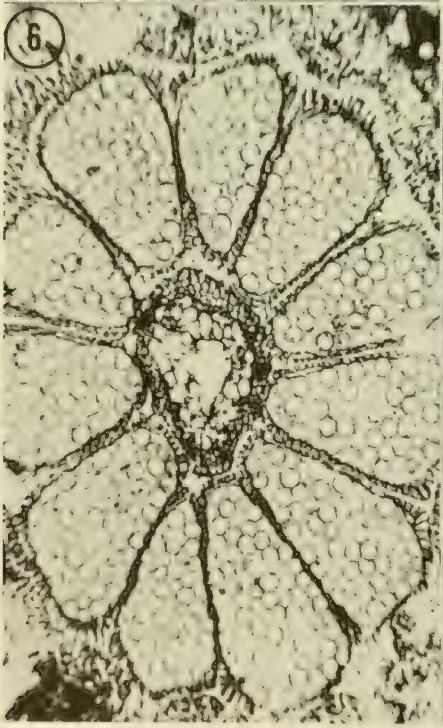
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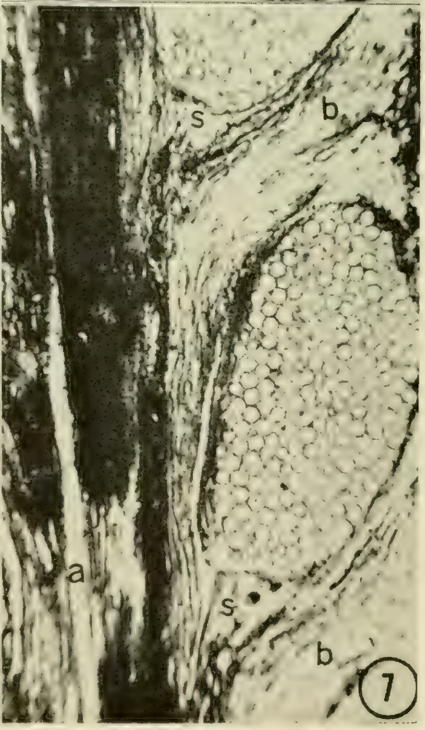
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outer sporangium wall covers the entire surface of the sporangium and also extends downwards along the abaxial side of the sporangiophore (Figs. 2, 8) with the result that some tangential sections of the cone seems to show sporangia with considerable sterile tissue inside the wall at the lower end (Figs 9, 11). The "sterile tissue" is, of course, only the obliquely sectioned apex of the sporangiophore, which is here surrounded by that portion of the sporangium wall which extends down its abaxial surface.

The number of sporangiophores and sporangia per whorl is apparently subject to considerable variation, not only possibly in different cones but also at various levels of the same cone. Among our 9 different specimens the number of sporangia per whorl varied from 8 to 14 with some sections showing the intermediate numbers of 9, 10 and 11 (Figs. 4, 5, 6).

In contrast to Mamay's (1954) type specimen and Reed's (1956) subsequent description of additional specimens, none of the present material shows the supposedly typical trimerous pattern of six sporangia and 12 bracts per whorl. This may possibly be correlated with the fact that Mamay's original cone (and possibly Reed's also) was an apical fragment where the number of parts per whorl seems to become smaller, possibly as a result of diminishing, determinate growth of the apical meristem. For example, one of our cones which was exposed for over 2.5 cm showed a whorl of 14 sporangiophores near the base, several whorls of 11 near middle and a whorl of 8 at the top. As this fragmentary specimen of over 9 nodes and internodes length showed no evidence of tapering at either end, it must be assumed that its intact length must have been much more than 2.5 cm and that the trend of variation in the entire cone might be expected to be also greater than that shown in the fragment.

The spores: All of the sporangia of the numerous specimens studied (Figs. 1, 2, 3, etc.) were packed with spherical spores averaging 90 μ in diameter. The spore wall is of two layers with the outer exospore consisting of a tangled reticulum of threadlike thickenings covering a very thin, smooth (almost transparent) endospore membrane.* The exospore threads are sometimes fused as prominent ridges (Fig. 16) but their threadlike nature may be seen in median views where the tangled loops of the thickened strands are clearly evident (Figs. 17, 18). This exospore reticulum was apparently laid down subsequent to the separation of the tetrads as the trilete

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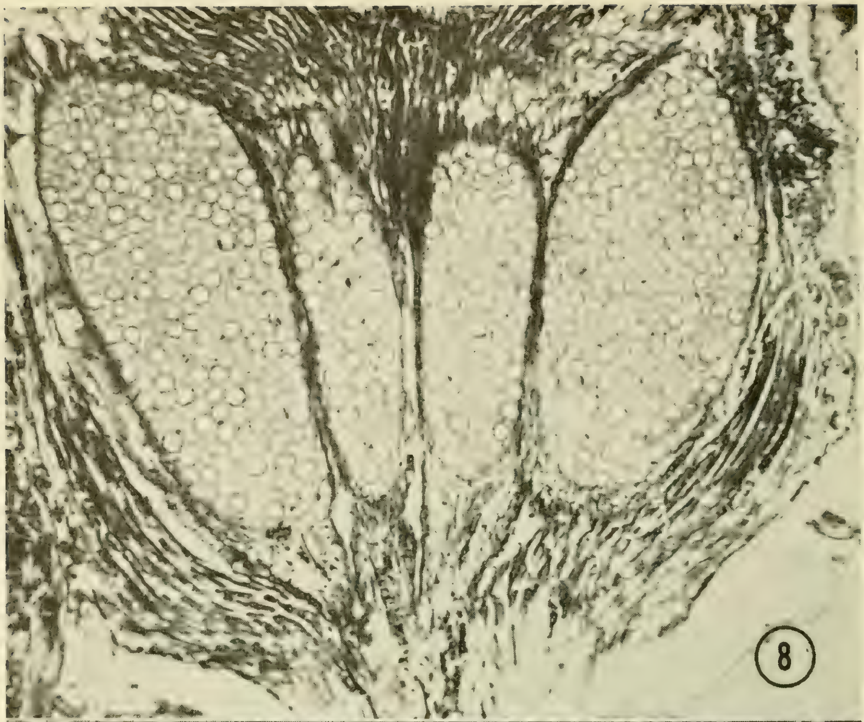
* While the terms *exospore* and *endospore* are used here (as in all prior descriptions), the terms *perispore* and *exospore*, respectively, possibly would be more proper as the former appears to have been formed after separation of the tetrads and the trilete scar is present only in the latter.

Figs. 4-7. *Litostrobus iowensis.* Fig. 4. Transverse section showing 14 sporangia in a whorl. X12. Fig. 5. Transverse section showing eight sporangia in a whorl. X12. Fig. 6. Transverse section with 11 sporangia in a whorl. X12. Fig. 7. Radial section. b, bract; s, sporangiophore; a, area of stele in center of axis. X12.



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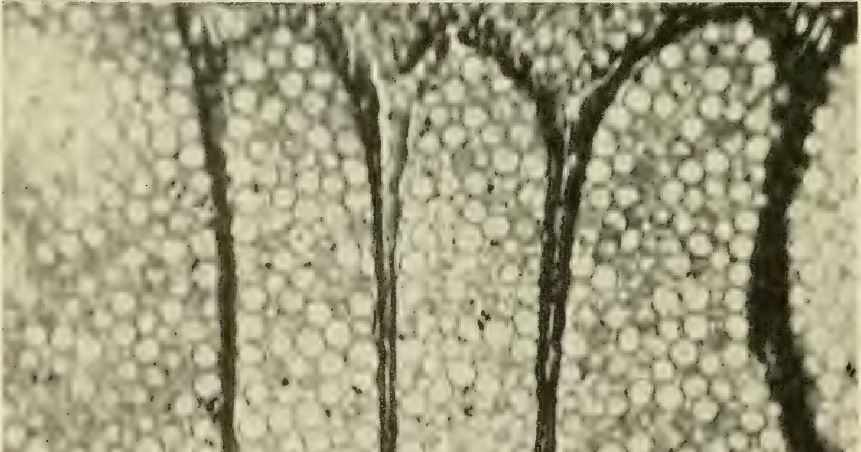

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scar on the proximal surface of the spore appears to be only in the smooth endospore wall although it may sometimes be visible through the exospore reticulum as shown in Mamay's Fig. 9.

The most unique character of the spores (remarked upon by Mamay in his original species diagnosis) is the presence of a circular groove on the proximal surface, clearly circumscribing the trilete scar, which seems to function as a dehiscence mechanism as both the exospore and endospore walls are ultimately shed in the area contained by it. The exospore wall is the first to go, thus exposing a circular area of the endospore about 60 μ in diameter. The exposed endospore membrane is marked by a centrally placed trilete scar, with three equal arms, each arm measuring 21 μ in length (Figs. 19, 20, 21). The endospore membrane, in the circular area, then breaks free leaving the round appertures shown in Figs. 20, 21. Most of the hundreds of spores observed had lost both the exospore and endospore walls within the area circumscribed by the dehiscence groove so that the trilete scar was still present on only a relatively few spores.

A feature of the exospore reticulum, which also deserves mention, is its apparent tendency to disintegration so that only rarely does it show the detail illustrated in Figs. 16, 17 and 18. The more usual state of preservation appears to be one in which the reticulate threads have become coalescent giving the impression of a membranaceous, ridged surface. In other cases the exospore wall may be lost completely, leaving only the smooth walled endospore, which in this condition resembles a spore of the *Calamospora* type with an average diameter of only 70 μ.

DISCUSSION

There can be no doubt that the cone specimens described here are assignable to the genus *Litostrobus* as established by Mamay (1954). There is complete agreement in the orthotropous sporangia, each terminating a single axillary sporangiophore, the character of the various cone tissues, and the unique spores. The points of difference (primarily those of number and arrangement of bracts and sporangiophores per whorl) are clearly variable in a single cone and consequently cannot even be used for distinguishing species.

The complicated vascular anatomy described by Reed (1956) presents more problems in that neither the present material nor the type specimen show any such structure. It is also the more remarkable in that while the specimens described here represent a stage of unusually fine preservation, Reed constantly emphasized that her material was poorly preserved. State-

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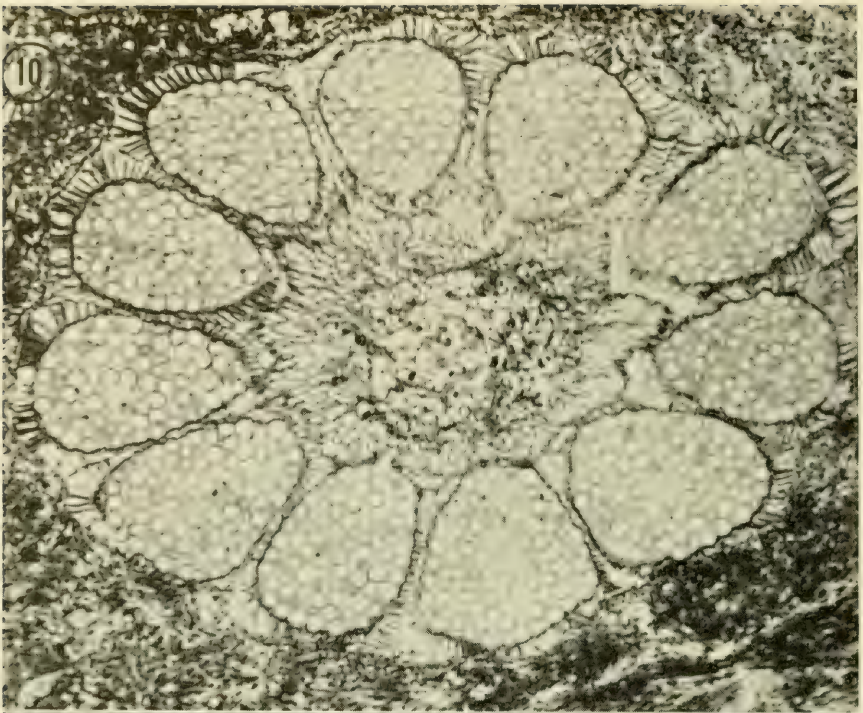
FIGS. 8-9. *Litostrobus iowensis*. Fig. 8. Longitudinal section slightly tangential to cone axis showing four erect sporangiophores with terminal sporangia. X25. Fig. 9. Tangential section of cone showing apparent "sterile tissue(s)" in sporangium because of oblique sectioning of apex of sporangiophore. X36.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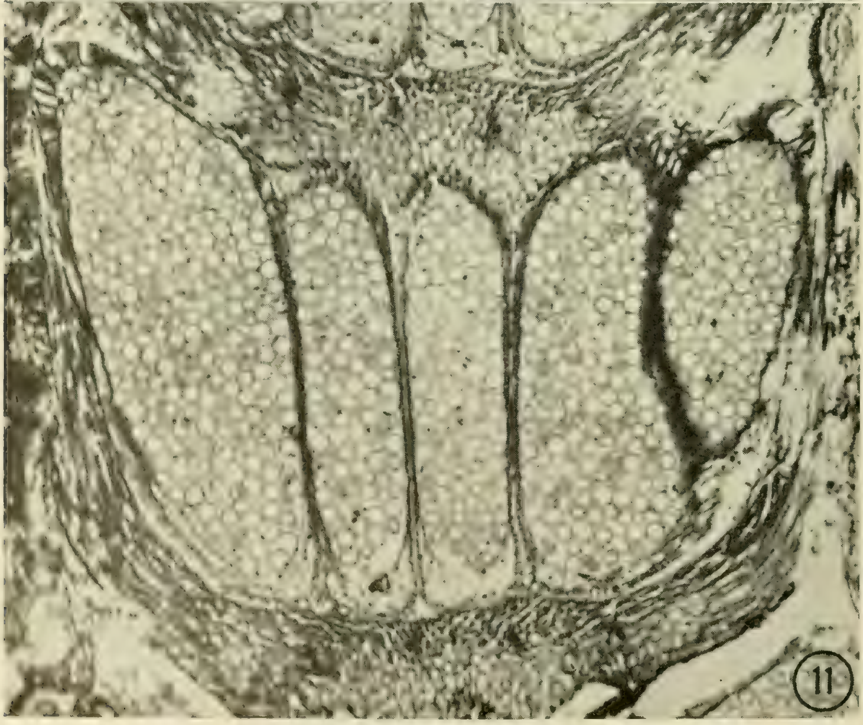
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ments such as, "Details of the stelar tissues are obscure because of poor preservation...," "The fragment is highly carbonized with the result that it possesses almost no cellular detail..." and "...the axis of the strobilus is poorly and incompletely preserved..." occur frequently. I have had the opportunity also to examine a number of the specimen peels cited by Reed and have been unable to see any such vascular branchings as were described.

It also seems significant that while Reed's triple dichotomy with bracts of the "first order" and "second order" is based completely on the concept of a constant trimerous system, i.e., parts in multiples of three, our material shows that no such constancy in numerical order exists. Certainly whorls of 8, 10, 11 and 14 could hardly be vascularized by a system based on a triple dichotomy of traces.

Not only do the present specimens show clearly that the sporangiophore trace arises directly from the stele axis and passes directly up to the base of the sporangium, but the sporangiophore trace is shown to be a much larger strand (8-10 tracheids vs. 2-3) than that in the bract, a condition which hardly seems likely if the sporangiophore trace arose as the final branch of a triple dichotomy. Accordingly, the simplicity of the structure of *Litostrobus,* first emphasized by Mamay, seems to be verified.

While the evidence would seem to indicate that Reed's concept of the vascular anatomy of *Litostrobus* was in error, her reconstruction of the cone showing short, sub-globose sporangia is certainly different from our specimens and Mamay's holotype. At the same time Reed's specimens present striking similarities to Leisman's (1964) cone of *Mesidiophyton* which, possibly significantly, is from essentially the same Kansas locality and horizon. The cone of *Mesidiophyton,* the stems of which Leisman (personal communication) now believes to be indistiguishable from *Sphenophyllum,* has the same basic structure as *Litostrobus* with whorls of orthotropous sporangia subtended by partially fused bracts. Leisman, however, felt that it was generically distinct in the following characters: (1) A trimerous symmetry for *Litostrobus* vs. whorls of 8, 10 and 11 in *Mesidiophyton.* (2) Twice as many bracts as sporangiophores in *Litostrobus* (both alternate and opposite) vs. the same number of bracts as sporangiophores in an alternate arrangement in *Mesidiophyton.* (3) Supperposed position of bracts and sporangiophores in successive whorls in *Litostrobus* vs. alternate position in *Mesidiophyton.*

It is immediately apparent that the variability now known to occur in *Litostrobus* is more than sufficient to account for all of the above supposed generic distinctions. For example, we now know that *Litostrobus* shows a variation in parts per whorl, of 6 to 14 with the entire range perhaps occurring in a single cone. Possibly as a direct result of this variation in number of parts

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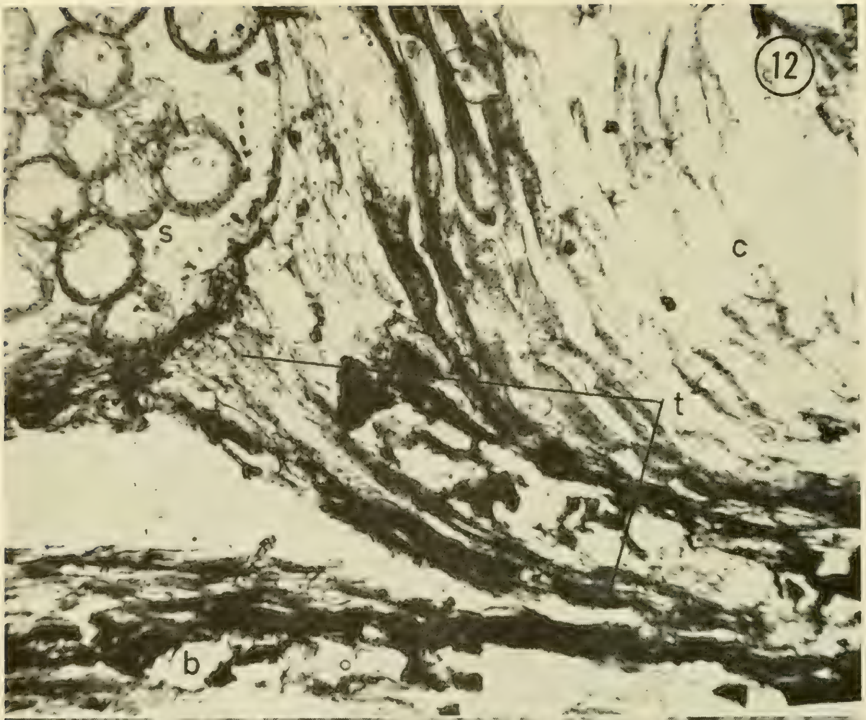
FIGS. 10-11. *Litostrobus iowensis.* Fig. 10. Transverse section of cone near base of bract disc. X20. Fig. 11. Tangential section showing overlapping of bracts of successive nodes and apparent "sterile tissues" in sporangia. X23.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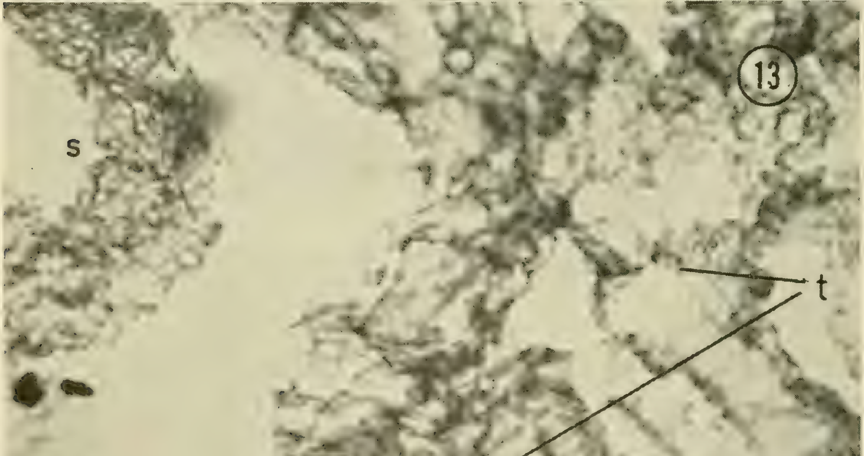
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from node to node there is also variation in the proportion and arrangement of the bracts and sporangiophores in successive whorls, i.e., alternate vs. superposed, etc. Figs. 1 and 6 show bracts equal in number to the sporangia and alternate with them. Other whorls, however, show occasional bracts opposite as well as alternate with the sporangia so that the number of bracts was sometimes greater than the sporangia. It is also obvious that superposition of parts in successive whorls is only possible where the number per whorl remains the same, while a change in number of parts in successive whorls would produce at least some alternate arrangement.

The *Mesidiophyton* and *Litostrobus* cones are, in addition to the axillary, orthotropous sporangia, also essentially identical in all of the following points: (1) Size of cone as a whole; (2) Size of the cone triarch stele; (3) Adaxial position of sporangiophore trace; (4) Abaxial position of melasmatic strand in sporangiophore; (5) Extension of sporangial wall downwards along abaxial surface of sporangiophore.

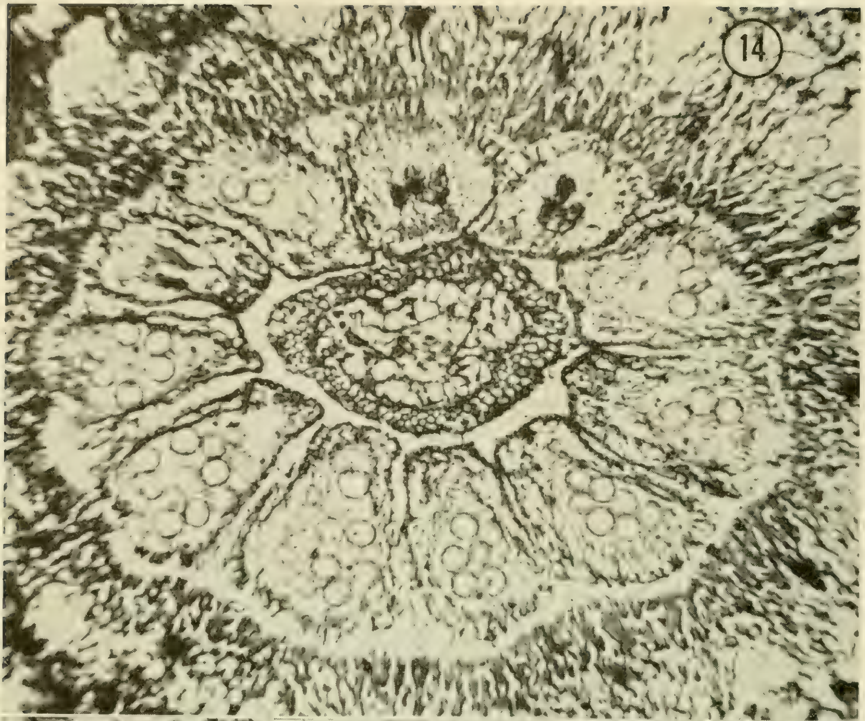
Accordingly there no longer seems to be any basis for not considering the cone specimens described by Leisman as falling within the generic limits of *Litostrobus,* although the following minor differences seem sufficient to justify recognizing it as a distinct species: (1) Globose to sub-globose sporangia 0.4-0.7 mm in diameter vs. elongate sporangia 1.2 mm long by 0.8 mm wide in *L. iowensis;* (2) Cone axis with thick cortex with *Sphenophyllum* like furrows and ridges vs. thin smooth cortex in *L. iowensis;* (3) Spherical spores with trilete scar but lacking circular, dehiscence groove found in *L. iowensis.*

If we now consider the above characters which seem to distinguish Leisman's Kansas specimens of *Mesidiophyton* from the Iowa specimens represented by Mamay's holotype and the present material, we find that the cone fragments described by Reed (1956) from Frontenac, Kansas, agree most closely with Leisman's specimens and not Mamay's *L. iowensis.* Accordingly, based on the observations of Reed's material and her own descriptions, it is felt that her specimens and Leisman's *Mesidiophyton* cone should be assigned to a distinct species of *Litostrobus* rather than the type species which so far seems to occur only in Iowa coal balls. Here again, however, it should be noted that Leisman's several cones show a simple, direct passage of vascular traces from the cone axis into the sporangiophores and bracts rather than the triple dichotomy described by Reed. The following emmended diagnosis and reassignments are as follows:

Litostrobus iowensis Mamay, emend. Baxter.

1956. *Litostrobus iowensis* Mamay, emend. Reed. Phytomorphology, 6:261-272.

FIGS. 12-13. *Litostrobus iowensis.* Fig. 12. Longitudinal section showing direct passage of vascular trace into sporangiophore. b, bract; t, trace; c, cortex of axis; s, sporangium and spores. X120. Fig. 13. Enlargement of portion of above. s, spore in sporangium; t, expanded apex of sporangiophore trace with tracheids showing scalariform and spiral thickenings. X520.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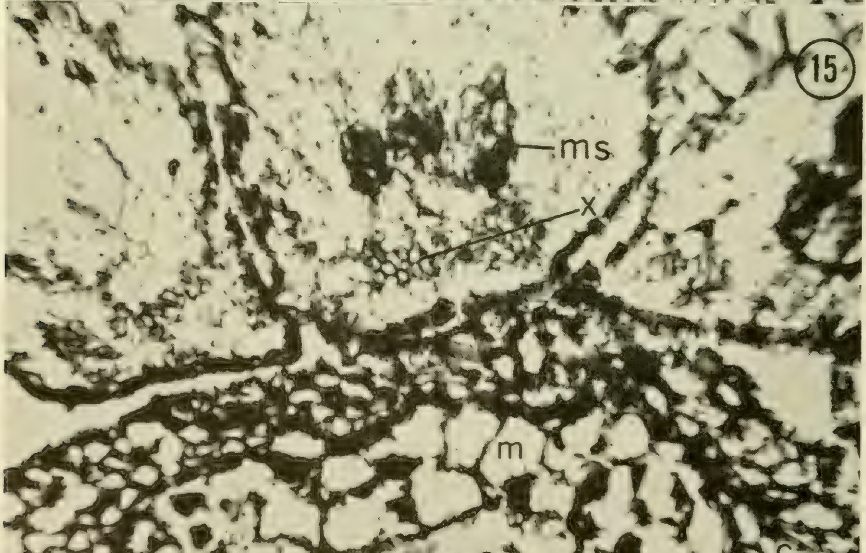
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GENERIC DIAGNOSIS—Cone verticillate, each node bearing a whorl of bracts and axillary, unisporangiate, pedicelate, orthotropous sporangia. Epidermal cells of bracts showing sinuous interlocking outlines. Number and arrangement of organs per whorl variable, decreasing in number towards the apex. Triarch, exarch, protostele; protoxylem with annular and spiral thickenings, metaxylem with multiseriate bordered pits.

SPECIFIC DIAGNOSIS—Cone small, up to 4-5 mm in diameter. Triarch protostele about 320 μ measured from adjacent protoxylem points, metaxylem with very thin walled tracheids. Melasmatic zone of tubular cells containing opaque "resin" surrounding stele. Cortex consisting of empty rectangular cells, 270 x 40 x 65 μ with thin smooth walls. Bracts and sporangiophores in whorls of 6-14 or more. Erect, axillary sporangiophores 0.4-0.7 mm long by 0.2 mm wide at base to 0.4 mm at flaring apex. Sporangiophore trace on adaxial side with a melasmatic strand abaxial to it. Sporangia ovoid, up to 3 mm long by 1.2 x 0.8 mm wide. Spores spherical with average diameter of 90 μ. Exospore of a tangled, threadlike reticulum, endospore memberane smooth, translucent with a trilete scar surrounded by a circular "dehiscence groove."

Litostrobus paulus (Leisman) Baxter.

1956. *Litostrobus iowensis.* Reed, Phytomorphology, 6:261-272.
1964. *Mesidiophyton paulus* (Cone). Leisman, Palaeontographica, 114B:135-146.

Cone similar to *L. iowensis* except in the following characters: Sporangia globose to sub-globose, 0.4 to 0.7 mm in diameter, cone axis with alternate ridges and furrows in outer cortex, spores apparently lacking "dehiscence groove" and having a sightly smaller size range of 55-80 μ which possibly may be due to loss of exospore wall.

Since it now seems certain that the stems attached to the *Litostrobus* (*Mesidiophyton*) *paulus* cones are indistinguishable from *Sphenophyllum,* there can no longer by any doubt of the sphenophyllalean affinity of the cone genus. We are thus again confronted with the problem of the extreme diversity of cone types apparently borne on *Sphenophyllum* stems, ranging from the exceedingly complicated structure of *Peltastrobus reedae* (Baxter, 1950; Leisman and Graves, 1964) and *Bowmanites fertilis* (Leclercq, 1936) to the relatively simple *Bowmanites moorei* (Mamay, 1959) and *Litostrobus.* The problem is further compounded in that, not only do we have at least four cone genera containing 35 species (Boureau, 1964) all attributed to one or two species of *Sphenophyllum* stems, but the evidence of our present material of *Litostrobus* seems to indicate a considerable variation in number

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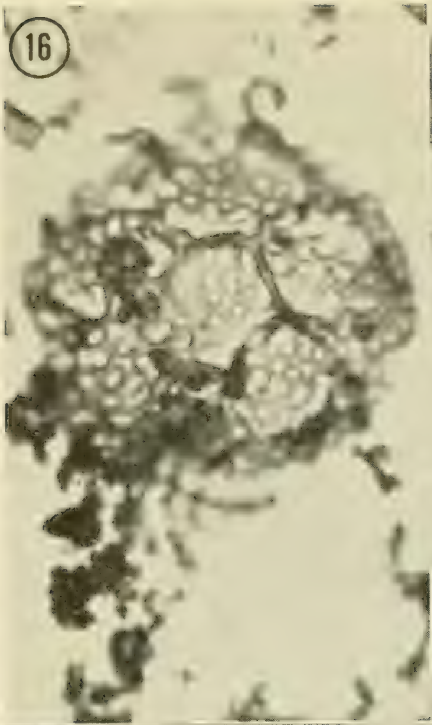
FIGS. 14-15. *Litostrobus iowensis.* Fig. 14. Transverse section of cone near base of internode showing cone axis in center surrounded by whorl of 11 sporangiophores just below their attachment to sporangia; the fused bract disc outside. X21. Fig. 15. Enlargement of top-center area of above. s, area occupied by stele (here poorly preserved); m, melasmatic tissue of cone axis; c, cortex of cone axis; x, adaxial xylem at apex of sporangiophore; ms, melasmatic strand on abaxial side of sporangiophore trace. X65.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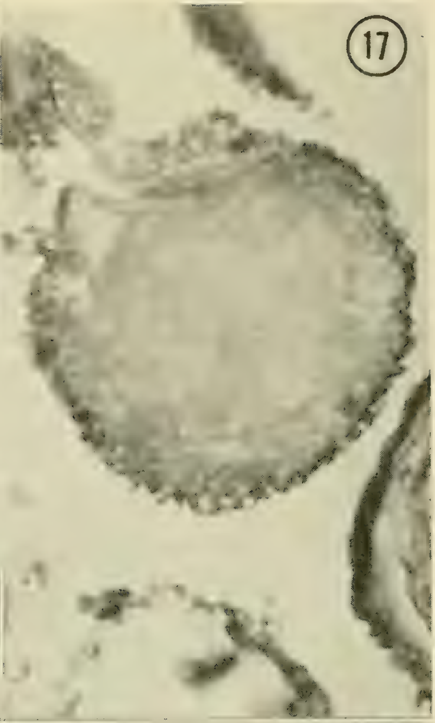
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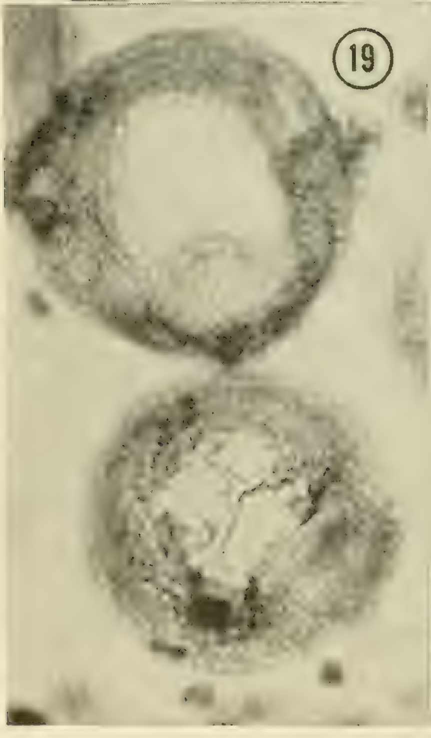
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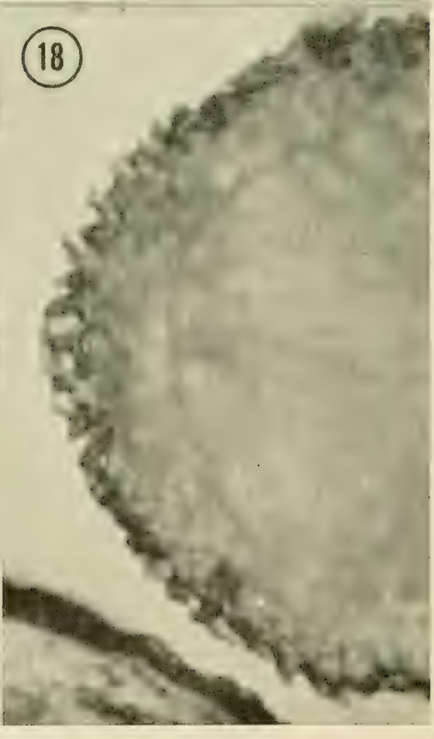
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and arrangement of sterile and fertile parts (which variations have previously been used as specific, or even, generic characters) within successive whorls of individual cones.

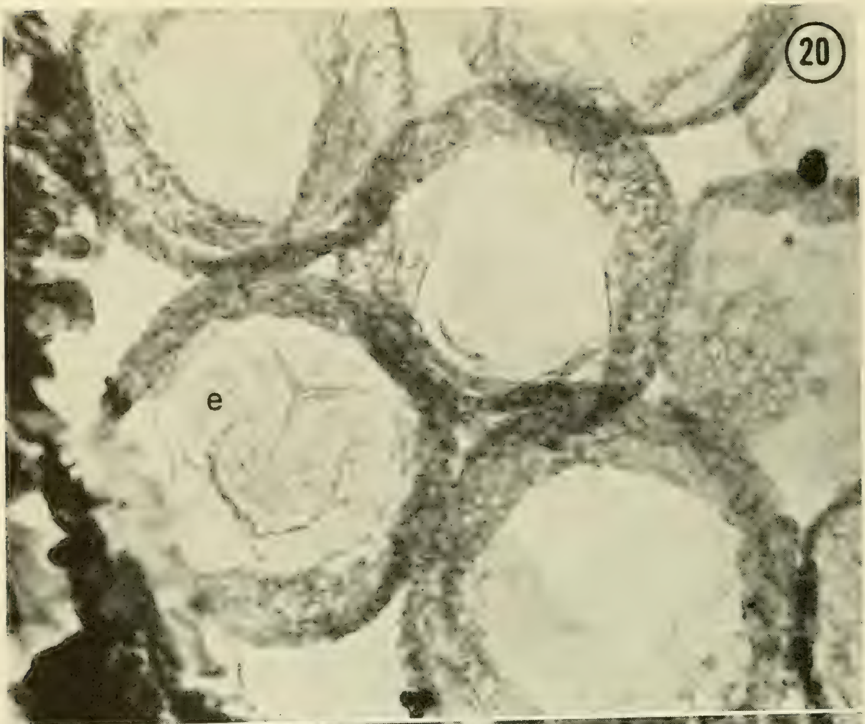
While it has now been recognized for some time that such a basic anatomical structure as the stele in *Lepidodendron* might vary from a protostele to a siphonstele in the same stem (Eggert, 1961) and the number of steles in the pteridosperm, *Medullosa,* might vary from three to over 11 in the same stem (Delevoryas, 1955), it was not uncommon for a number of early investigators to consider these variations as specific or generic differences.

In a similar way we now have a considerable assemblage of supposedly distinct taxonomic entities based on sphenopsid fructifications in which it may very well be that equivalent heteromorphic forms occur. For example, the enigmatic cone, *Sphenostrobus thompsonii* (Levittan and Barghoorn, 1948), which has been recognized by both Mamay and Leisman as having a number of features in common with *Litostrobus,* could conceivably be merely a basal fragment of the latter genus. The main distinguishing characters are the tetrarch stele in *Sphenostrobus,* its larger number of bracts and sporangia per whorl, and the sessile nature of the sporangia.

It is not the intention here to do more than suggest that the range of polymorphism which seems apparent in *Litostrobus* might include a larger, more basal region with the characters of *Sphenostrobus.* It should be stated, however, that there is also a (previously unreported) striking similarity in the spores of the two genera as well as the distinctive melasmatic zone in the cone axis.

While the triarch protostele has so far seemed basic to *Sphenophyllum* axes, the number of protoxylem points of protosteles in living plants (roots) is known to be subject to frequent variation. In the common *Ranunuclus acris* root, for example, triarch, tetrarch and pentarch conditions may all be found.

Figs. 16-19. *Litostrobus iowensis.* Spores. Fig. 16. Spore with reticulate exospore. X500. Fig. 17. Optical-median view of spore showing reticulate strands of exospore in side view. X500. Fig. 18. Enlargement of area of above. X850. Fig. 19. Spores with partial disintegration and shedding of exospore. Bottom spore shows trilete scar on smooth endospore wall. X420.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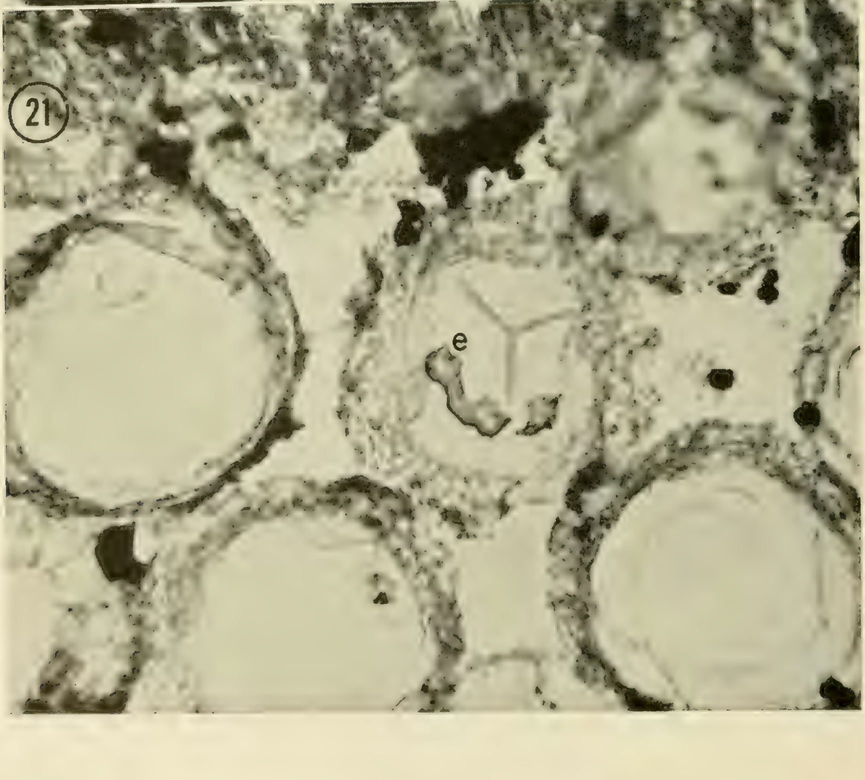
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FIGS. 20-21. *Litostrobus iowensis*. Spores showing "dehiscence area" formed by shedding of circular section of exospore followed by underlying endospore. Spores with trilete marks still have endospore(e). Those lacking scar have open "dehiscence" apperture. X500.

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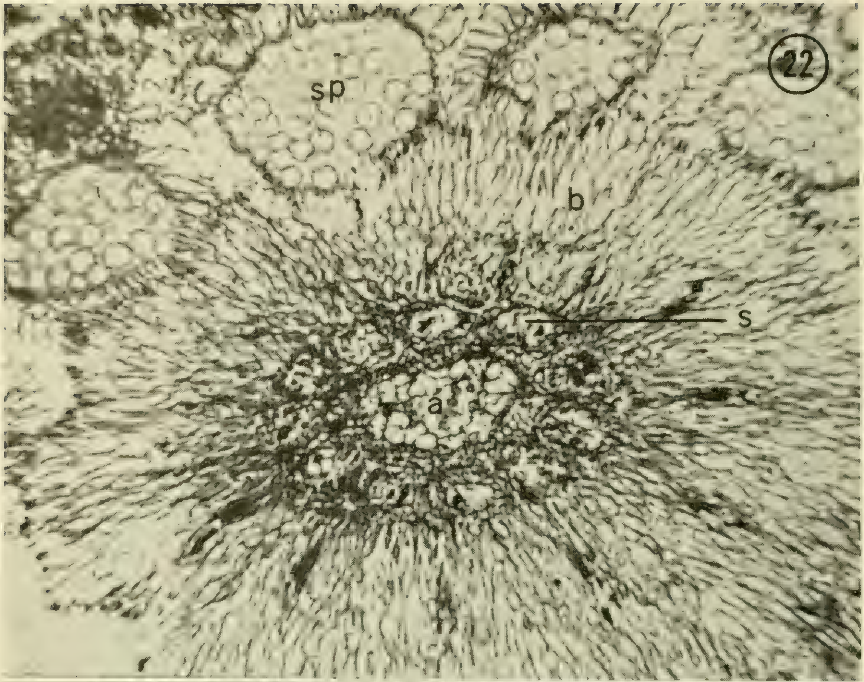

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Figs. 22-24. *Litostrobus iowensis*. Fig. 22. Transverse section of cone showing elongate sporangia of lower whorl extending above the fused bracts of the next higher whorl. Compare to Fig. 2. Sp, tips of sporangia of lower whorl; b, disc of fused bracts; s, sporangiophores of next higher whorl; a, cone axis. X20. Fig. 23. Free lobe of a single bract. X25. Fig. 24. Metaxylem tracheid with reticulate arrangement of round bordered pits. X375.

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

FLORAL MORPHOLOGY AND SYSTEMATICS OF *PLATYSTEMON* AND ITS ALLIES *HESPEROMECON* AND *MECONELLA* (PAPAVERACEAE: PLATYSTEMONOIDEAE)

By

Wallace R. Ernst

SMITHSONIAN
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Vol. XLVII Pages 25-70 March 3, 1967 No. 2

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. XLVII Pages 25-70 March 3, 1967 No. 2

Floral Morphology and Systematics of *Platystemon* and its Allies *Hesperomecon* and *Meconella* (Papaveraceae: Platystemonoideae)

By

Wallace R. Ernst*

ABSTRACT

The five species of subfamily Platystemonoideae, primarily in California, are compared for morphological structure and variation. They are contrasted with other Papaveraceae to show evolutionary relationships and as background for a taxonomic treatment. Information is assembled from field, culture, herbarium, and computer method studies.

INTRODUCTION

Comparative knowledge of form and structure, in addition to providing the basis for logical systematics and taxonomy, also is provocative from an evolutionary point of view. Many clusters of species of Papaveraceae can be arranged in various sequences ranging from the complicated to the simple, or the reverse, on the basis of morphological patterns in floral vasculature. As for the actual direction of evolutionary changes among the ancestors of these plants, the arguments often are about as valid for one sequence as for another. Simplicity of structure in many cases may just as well be due to advancement or reduction as to antiquity; and complexity may as well be attributed to multiplication of parts as to primitiveness. Surely, these sequences imply evolutionary proximity among the taxa exhibiting them but many questions concerning phylogeny cannot be answered without other kinds of information.

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* Department of Botany, Smithsonian Institution, Washington, D.C., and The University of Kansas, Lawrence.

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The subfamily Platystemonoideae, comprised of *Platystemon, Hesperomecon,* and *Meconella,* is one of four major lines of development in Papaverceae. The other subfamilies are Chelidonioideae, Eschscholzioideae, and Papaveroideae, which are distinguished on the basis of floral morphology, pubescence, pollen, and seeds (Ernst 1962a, b). Such well known genera as *Corydalis, Dicentra, Fumaria,* and their immediate allies are not included in this conception of the family but form the related family Fumariaceae.

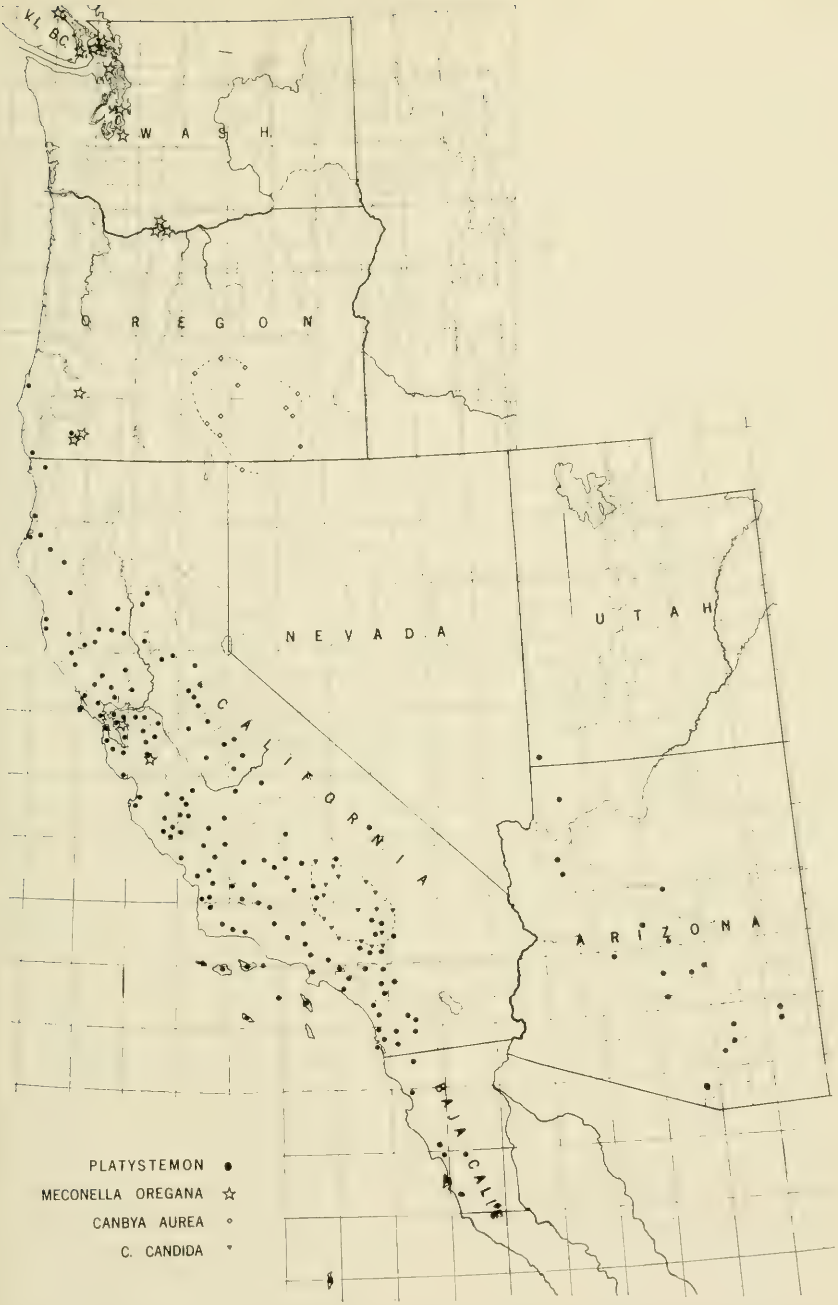
The objective of this paper is an improved taxonomy. The commentary purports to explain evolutionary relationships among the taxa of subfamily Platystemonoideae and the relationship of this complex of species to other Papaveraceae. These taxa have been studied in conjunction with my morphological survey of the family. Since opinions have differed substantially on systematic arrangement of these and other taxa of Papaveraceae, it was thought that a detailed examination of floral morphology would bring to light some less conspicuous structural features for comparison. Wild populations of all species have been studied throughout much of their natural ranges and representatives of all species have been examined cytologically and cultivated. These observations have been supplemented by examination of herbarium specimens from more than 20 herbaria. The following commentary concludes with a taxonomic treatment of subfamily Platystemonoideae.

ACKNOWLEDGEMENTS

Among the many persons who have aided me in this study are M. A. Canoso, R. H. Eyde, R. S. Ferris, A. J. Hill, J. T. Howell, R. C. Jackson, T. Koyama, H. Lewis, M. E. Hale, T. F. Niehaus, R. Ornduff, R. N. Philbrick, P. H. Raven, R. L. Taylor, J. H. Thomas, H. J. Thompson, and E. C. Twisselmann. I thank the curators of the herbaria where I have visited or borrowed specimens. Part of the research presented in this paper was carried out while I was a graduate student at Stanford University.

MATERIALS AND METHODS

Natural populations of the plants mentioned in this paper were observed in Arizona and Oregon as well as in many parts of California. When feasible, cytological fixations and herbarium voucher specimens were collected. A list of collections studied in detail and cultivated for at least one season at Stanford University appeared in Ernst (1958, p. 114). The first set of these collections is deposited at Stanford University and duplicates also are available at the University of California, Berkeley; California Academy of Sciences, San Francisco; and Rancho Santa Ana Botanical Garden, Claremont. Besides the herbarium materials in these institutions I also have examined


V.I.
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WASH.
OREGON
NEVADA
UTAH
CALIFORNIA
ARIZONA
BAJA CALIF.
PLATYSTEMON ●
MECONELLA OREGANA ☆
CANBYA AUREA ○
C. CANDIDA ▾

FIG. 1. Distribution of *Platystemon californicus, Meconella oregana, Canbya aurea,* and *C. candida.* Northernmost locality is Jesse Island off Vancouver Island, British Columbia; northern cluster of islands off Southern California, left to right, San Miguel, Santa Rosa, Santa Cruz, and West Anacapa; next cluster south, left to right, San Nicolas, Santa Barbara, Santa Catalina, and (no record) San Clemente; southernmost locality is Guadalupe Island, Mexico.

specimens from ARIZ, BH, BM, CU, E, GH, JEPS, K, LA, MO, NY, OBI, ORE, OSC, ND, PH, POM, SBBG, SBM, SD, UCSB, US, WILLU, WS, WTU.

The chromosome numbers were reported earlier (Ernst, 1958) and no new data are added here. It should be noted, however, that the chromosome number for *Hesperomecon linearis*, n=7, is based upon earlier reports for this species under the name of *Meconella linearis*. The illustrations are from camera lucida tracings of materials fixed in 3:1 ethanol-acetic acid and squashed in acetocarmine (Figs. 6, 7). Unless otherwise indicated, the figures represent meiotic divisions of pollen mother cells.

The floral diagrams represent architectural patterns of primary xylem and were prepared from young flowers cleared in lactic acid (Figs. 4, 5, 8, 9, 11). The materials used are from my own collections. The flowers were cleared after some preliminary wetting or bleaching treatment such as carnoy solution. If they were from pressed and dried herbarium specimens, they were first moistened with alcohol or water. Larger or darkly colored flowers sometimes required prolonged soaking in mild potasium- or sodium-hydroxide solution after which they were washed in water and placed in lactic acid. It was advantageous to examine younger materials in polarized light as newly formed secondary thickenings on cell walls glowed conspicuously and developmental stages of tracheary tissues could be compared. The examination of whole cleared flowers often revealed details in structure and proportion that are lost when one only studies sections of materials embedded in paraffin.

The diagrams show the flowers as though cut longitudinally and flattened. Unfortunately, the position and relative sizes of the organs are somewhat distorted; however, an attempt was made to keep the distortions relatively consistent. Certain problems must be acknowledged in this kind of two dimensional representation of transparent or translucent three-dimensional subjects. Among the foremost of these is that no two flowers, even from the same plant, were precisely the same and some of the illustrations concern very small structures which sometimes were difficult to observe. Since several collections or several flowers have been examined for each species, it is hoped that the diagrams are representative of the typical structure. There were exceptions and not all of those observed have been reported. Floral morphology should be thought of as dynamic in the sense that changes in structure and proportion are continuous from meristematic initiation until abscission. Even after cessation of active growth, changes that occur with aging and drying-out must be expected. Eames (1961, pp. 87, 229) appropriately cautions that floral organs, for comparative studies, only are differentially mature at the time of anthesis but this should not discourage the study of developmental phenomena. The distinctive developmental patterns in

Platystemonoideae and especially in *Meconella* serve as examples since they soon are obliterated and lead to rather similar knots of tracheary tissues in the receptacles of older flowers.

A discussion of floral morphology is made more difficult by the problem of applying consistent names to structures, particularly in the dynamic phases of development. A clear account of trace in particular is not possible and one must resort at times to vein as well as to bundle and trunk in an attempt to distinguish more or less equivalent portions of the vascular supply. Confusion arises in describing the vascular supply of the gynoecium when one must compare a single (but theoretically duplex) placental bundle (or vein) with a pair of adjacent ventral veins (or bundles) which might be somewhat joined only basally. A placental bundle and a pair of ventral veins to adjacent carpel margins are homologous except that the latter are not completely fused. A distinction between trace and vein (or bundle) sometimes is difficult because the vein part often differentiates before the trace part can be seen or before it is completely connected with the remainder of the vasculature of the receptacle. It is hoped that the diagrams will clarify these points.

THE PLATYSTEMONOIDEAE

Over half a century ago a monograph of *Platystemon, Hesperomecon,* and *Meconella* was published by E. L. Greene (1903), who included a total of 64 species, most of which he described as new. Soon afterward Fedde (1909) revised these taxa and increased the number of species to 71 plus some infraspecies. When Jepson (1922) studied the same taxa he reduced the number to three species and a few varieties and placed them in two genera. A more satisfactory account was presented by Abrams (1944) who, for the first time, adequately circumscribed the species. In my opinion there only are five species and while I employ the same specific limitations used by Abrams, I find myself more in agreement with Greene concerning the relegation of the species to genera.

Platystemonoideae are indigenous to the western United States and, in particular, to California where all occur and three are endemic or very nearly so. They are colonial, low, tufted, obligate vernal annuals. When elongated flowering shoots are produced, the leaves on these are opposite or whorled and usually reduced in size. The lower leaves more or less are alternate. The inflorescences are terminal, determinate, and more or less scapiform. The buds nod and the erect flowers, which close at night, are borne on relatively long peduncles and have trimerous perianths with three sepals and a total of six petals inserted in two cycles; the outer petals are a little larger than the inner ones. The staminal filaments frequently are expanded or toothed; the pollen is tricolpate. The gynoecia are superior, composed of three or more carpels and are syncarpous but with separate stigmas.

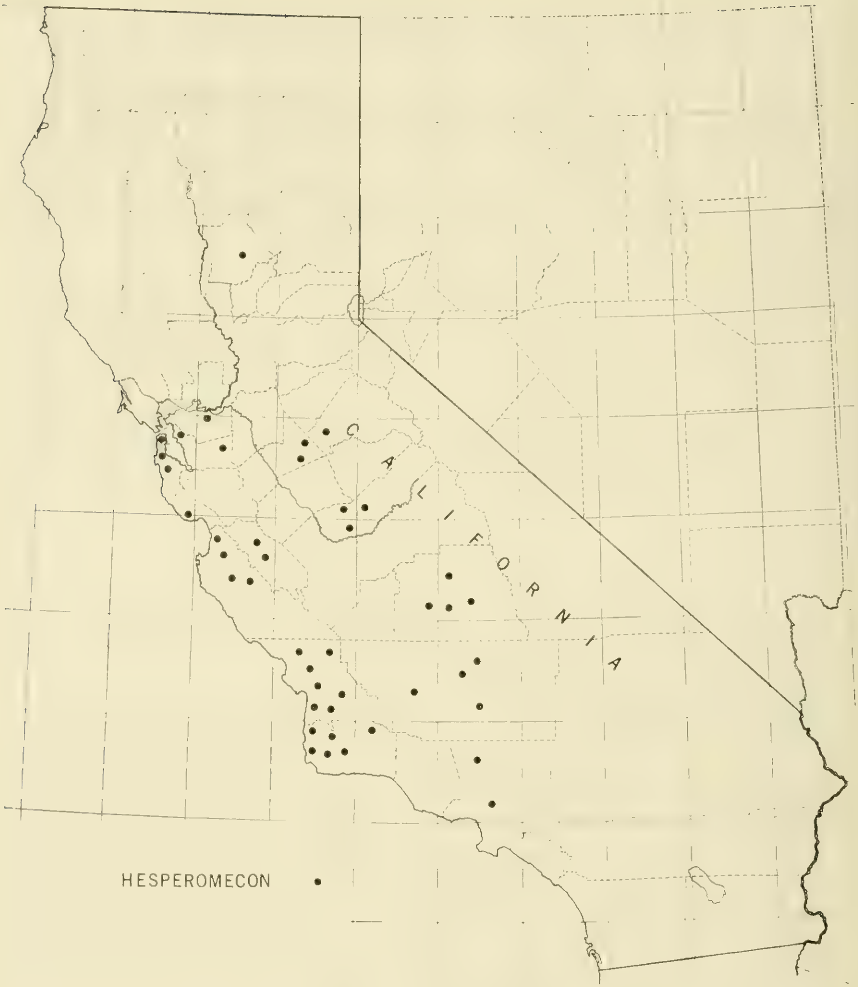


Fig. 2. Distribution of *Hesperomecon linearis*. Northernmost locality is in Butte County; southernmost in Los Angeles County.

Many morphological features are shared by *Platystemon, Hesperomecon,* and *Meconella,* the most important being the characteristics of the gynoecia, which at once unite the subfamily and, at the same time, distinguish the genera. Unlike all other Papaveraceae, the species in these genera do not form intracarpellary valves in the fruit walls for seed dispersal, but rather whole carpels, each with its discrete stigma attached, disassociate at maturity by cleaving through the placental region of the fruits. The subfamilial rank of Platystemonoideae is in recognition of the uniqueness of this situation in

Papaveraceae. One cannot say from the evidence preserved in present day plants whether the valves, so characteristic of the remainder of the family, never developed in the phylogenetic sense, or whether they were developed and have since been lost. Ontogenetically, the family is syncarpous in respect to non-vascular tissues, and the apocarpouslike vascular structure with the absence of valves in these species may be an example of a neotonic innovation.

The only member of Platystemonoideae that is well known to taxonomists is *Platystemon.* Its relative position within Papaveraceae has been given by many authors, beginning with Bentham's (1834) original description, as borderline between Rhoeadales and Ranales for some combination of the following characteristics: the perianth is trimerous; the anthers are numerous and spirally arranged; the carpels are many and more or less separate or only loosely coalescent, or essentially apocarpous. This allusion to its relationship and alleged structure usually has not been accompanied by documentation, and my observations do not support the above phylogenetic position as the only possible interpretation. The insertion of the perianth with twice as many petals as sepals and the petals in two cycles, as well as the specialized and dissimilar margins of the sepals (Figs. 5A; 8E), clearly fixes *Platystemon* in Papaveraceae. No convincing evidence is preserved in the floral morphology of contemporary Papaveraceae that either two- or three-merous forms, *per se,* are primitive. The abscission scars of the stamens externally on the receptacle may seem to be spirally oriented but the traces to the scars originate in no particular order (Fig. 4A). The gynoecium is syncarpous ontogentically and its apocarpous-like appearance more or less is superficial, becoming more conspicuous with later development and maturation (Fig. 5E, F, G). From the standpoint of the vascular supply to the carpels, the apocarpouslike structure is much more highly developed in *Meconella oregana* than in *Platystemon.* This situation is far more cryptic in *M. oregana* and has gone unnoticed since there is no suggestion in the external form of the gynoecium of the apocarpouslike internal pattern (Fig. 9G) and this species, although distinctive, is not well known to botanists.

Nothing is peculiar to the structure of flowers to show taxonomic rank but there is plenty of evidence for comparing degrees of similarity. On morphological grounds there are five basic taxa (species) in the *Platystemon-Hesperomecon-Meconella* complex. These occur only in western North America and they have no close relatives anywhere except, possibly, for the kind of limited parallelism in some genera of subfamily Papaveroideae. From the taxonomic point of view, these taxa fall into three essentially coordinate categories: there are three of *Meconella,* one of *Platystemon*, and one of *Hesperomecon.* This conflicts with the system used in most contemporary floras dealing with these species since *Hesperomecon linearis* is treated as a

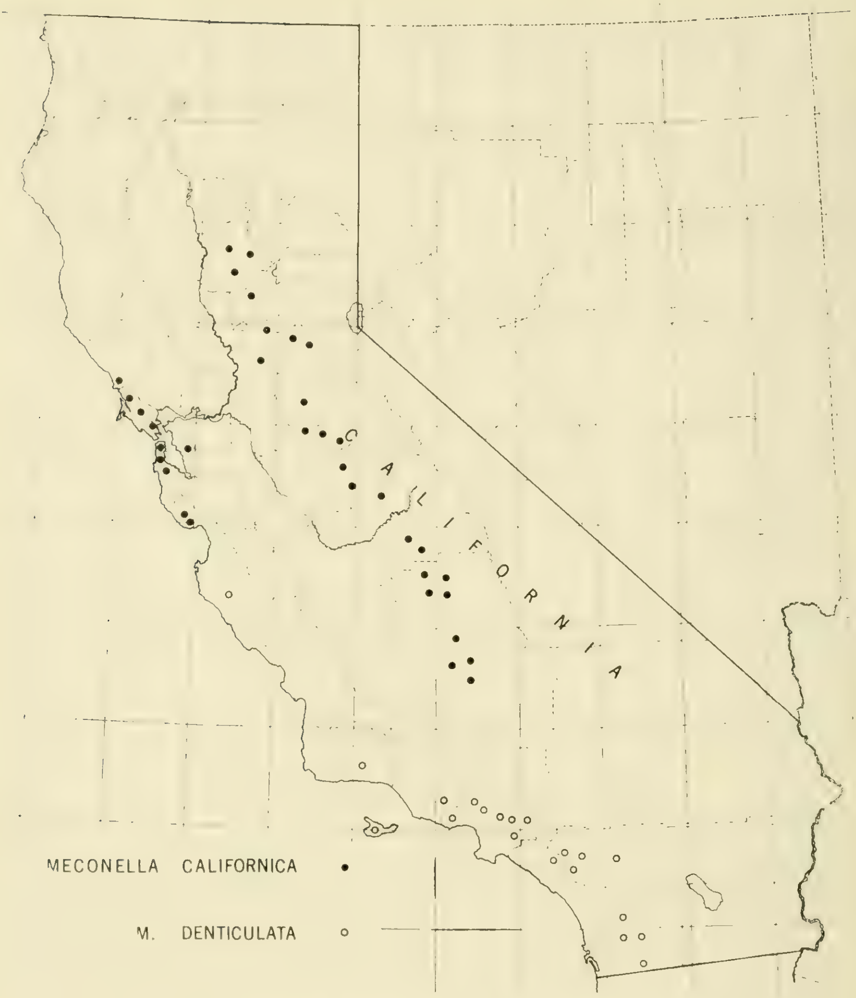


FIG. 3. Distribution of *Meconella californica* and *M. denticulata.* Northernmost locality is in Butte County; the only insular locality is Santa Cruz Island; the southernmost locality is in San Diego County.

species of *Meconella,* i.e., *M. linearis.* The critical element is *Hesperomecon linearis* which has as much or more in common morphologically with *Platystemon* as it does with *Meconella.*

A taxonomic system for these five species based on only two genera, *Platystemon* and *Meconella,* disregards obvious morphological relationships. Three coordinate genera or a single inclusive genus, *Platystemon,* is better. With the remainder of the family in perspective, recognition of three genera seems preferable to me but, in the final analysis, this is an arbitrary point and a single genus would be just as defensible on scientific grounds. My methods have led me to believe that these are the practical units of Platystemonoideae for taxonomic purposes. Additional taxa are not to be ruled out, but the criteria for defining them will have to be more sophisticated than mine.

Pubescent, linear leaves and linear cotyledons distinguish both *Platystemon* and *Hesperomecon*, but *Platystemon* has several carpels while *Hesperomecon* only has three. The species of *Meconella* are distinguished by their glabrous and distinctly spatulate basal leaves and by their minute, spatulate cotyledons. All species are diploid. The similarities between the species of Platystemonoideae and the two species of *Canbya,* subfamily Papaveroideae, will be discussed briefly but *Canbya* is not included in the general remarks. For brevity, since only one species is involved in either case, *Platystemon californicus* and *Hesperomecon linearis* often are referred to only by generic name. Synonomy follows Abrams (1944) except that *Meconella linearis* is treated as *Hesperomecon linearis.* Contrary to some earlier treatments, I find that the closest ally of *Meconella oregana* is *M. californica* and that these are distinct species. The combination *M. oregana* var. *denticulata* is misleading since *M. denticulata* stands somewhat apart from both *M. oregana* and *M. californica* in structure of gynoecium and in morphology and/or number of anthers.

Basic Affinities

The Platystemonoideae are a distinctive group of species whose affinities to other Papaveraceae are not altogether clear but there can be no question of their being Papaveraceae. In superficial appearance, the cespitose, more or less scapiform habit, the nodding buds with woolley sepals in *Hesperomecon* and *Platystemon* seem somewhat similar to subfamily Papaveroideae, especially to *Arctomecon,* to some species of *Papaver* and *Meconopsis,* and possibly also to *Canbya.* The closeness of the relationships, based upon these similarities, are difficult to estimate. The multicellular-multiseriate hairs, the well developed dissimilar margins of sepals, the tendency for suppression of the dorsal bundle in the carpels, and the tricolpate pollen would seem to confirm a relatively close affinity with Papaveroideae. The basic nature of the carpels with their free stigmas and total absence of commissural development, and the dehiscence of the fruits without typical valves, however, clearly isolate Platystemonoideae from Papaveroideae. Fruits predominately with only two carpels, differences in dehiscence mechanisms of the fruits and structure of pollen, hairs, and seeds also isolate Platystemonoideae from Eschscholzioideae and from Chelidonioideae. The Platystemonoideae seem to represent a separate line of development within Papaveraceae and, while the relationship may not be very close, they show some phenotypic similarities with subfamily Papaveroideae.

Geographical Distribution

From the distribution maps (Figs. 1, 2, 3) it is obvious that *Platystemon* is the most diverse ecologically since it covers the greatest geographical area and the greatest variety of habitats and altitudes. The range extends farther south and east than the other species, including at least seven of the Channel Islands off California, and at one time also Guadalupe Island, Mexico. It is not surprising that *Platystemon* is variable phenotypically and, apparently, it is not uniform cytologically.

The distribution of *Hesperomecon* is much less extensive than, but falls entirely within, that of *Platystemon*. Where *Hesperomecon* grows, one also expects *Platystemon* to be nearby. The two often seem almost to imitate one another in variability, and they are so similar phenotypically that specimens of both have been mounted on the same herbarium sheet, in some cases probably having been gathered in the same handful of plants.

The morphological gap separating *Meconella* from *Platystemon* and *Hesperomecon* is pronounced particularly in regard to leaf shape and, accordingly, specific resemblences are more remote. The species of *Meconella* are allopatric among themselves with one tentative exception. Some specimens from a few localities east of Berkeley, California, in the vicinity of the Alameda-Contra Costa county line, cannot be identified without some reservations. Perhaps the easiest solution to this taxonomic problem would be to consider the small petals and the fewer stamens of these plants as representing one of the extremes of *M. californica*. The variation within some of the collections, however, seems to bridge the gap between *M. californica* and *M. oregana,* whose next nearest locality to the north is in Oregon. Farther south in California a few specimens have been collected on the eastern slopes of the Mt. Hamilton Range in Santa Clara County, an area that is outside the range of *M. californica,* and these plants are rather definitely equivalent to *M. oregana*. Living plants in the Berkeley area have not been studied, but I submit that both *M. californica* and *M. oregana* might have occurred in this region, perhaps within cross-pollination distance.

Populations of *Meconella,* with only two near exceptions, do not occur in mixed colonies with either *Platystemon* or *Hesperomecon,* but they do grow on neighboring hillsides. For the most part *Platystemon* and *Hesperomecon* inhabit more open and exposed regions such as slopes or fields, and they span the communities from seaside dunes, woodlands, grasslands, to meadowlike areas, and *Platystemon* also occurs in arid desert margins. In those regions where the distribution of *Meconella* appears to overlap closely that of *Platystemon* and/or *Hesperomecon,* the species of *Meconella* are more likely to occur at somewhat higher altitudes on more moist to very wet banks, in sunny openings to be sure, but usually near shrubs and often in association with cryptogams such as terrestrial bryophytes and lichens as well as with species of *Dodecatheon, Plectritis,* Ranunculaceae, and Saxifragaceae. The species often are found near colonies of *Lasthenia.* The dates recorded on herbarium specimens for almost all species read from February to June. While this establishes a general vernal growth and flowering period, the dates themselves probably are less important than the altitude and annual fluctuations in seasonal rainfall and temperature. The ecological amplitude of *Meconella* seems more restricted than that of *Platystemon* and *Hesperomecon,* and *Meconella* occurs in the relatively earlier and wetter part of the spring-time, regardless of the date. By appearing early, the species are able to survive in plant communities such as chaparral or foothill woodland where digger pine and/or douglas oak predominate and where the substrates soon become hot and very dry.

Effective barriers between *Platystemon* and *Hesperomecon* are predicted since the characteristics of the two species are maintained where the two occur intimately in mixed colonies. They are similar but it is nonetheless difficult to visualize what compromises in structure of the gynoecia might be brought about by the impact of hybridity. Throughout most of its range *Meconella* seems to have somewhat different ecological requirements than *Platystemon* and *Hesperomecon.* It is notable, however, that *Hesperomecon* (normally with many stamens) and *Meconella californica* (usually with about 12 stamens arranged in two cycles of six each) began to resemble each other more closely in the foothills of the southern Sierra Nevada of California where the number of stamens in *Hesperomecon* may be reduced to about 10 (almost in two series) or sometimes only six, and *Meconella californica* may have as few as eight. Rather than being caused by the exchange of genetic materials between these two species, I think the similarities in appearance of the plants and reduced number of stamens is more likely due to parallel responses in these species to the progressively more extreme environments in which they are able to survive. One only can wonder if the conditions which brought about the increased phenotypic similarity in otherwise distinctive taxa might also enhance their potential for hybridization.

Under ordinary circumstances hybridization between *Meconella* and either *Platystemon* or *Hesperomecon* would seem unlikely from the morphological point of view; however, hybridization between any two species of *Meconella* would not seem to require profound adjustments in basic morphology. Although no interspecific crosses are available to demonstrate it, barriers may be less well developed among the species of *Meconella.* This is suggested by the allopatric distributions of the species, except for the single area where the characteristics of *M. oregana* and *M. californica* appear to blend and where plants of the two species might have occurred within pollinating distance. A note of caution must be interjected into these speculations because the literature does contain references to hybridization in such unexpected places as between *Papaver somniferum* (a caulescent, obligate annual with chromosome numbers of n=11 or 22) and *P. orientale* (an acaulescent herbaceous perennial with n=?14 or 21) according to Kawatani & Asahina (1959). Other hybrids equally surprising from both the taxonomic and morphological point of view have been reported for *Meconopsis*.

Cultivation

Representatives of the five species of Platystemonoideae were cultivated for at least three seasons in an open lathhouse at Stanford University. Like most Papaveraceae, the plants usually do not survive transplantation and new flowers seldom are initiated once the plants are disturbed. Transplants are more likely to be successful if they are only a few mm tall. No particular difficulty was encountered in growing either *Platystemon* or *Hesperomecon* from seeds sown in pots or in nursery flats of soil, and the plants reappeared year after year in the same containers without being resown. It was not possible to maintain cultures in the open ground.

The species of *Meconella* seemed more tempermental and frequently damped-off from one cause or another. Cultures were established by potting fruiting wild plants in a light, small gravel cover which seemed to provide better aeration at the base of the plants and also served to prop the plants upright. Seeds ripened from the transplanted specimens were allowed to fall directly into the gravel where they remained through summer and winter in the open lathhouse to germinate the following spring. The gravel seemed to keep the very small seeds from being splashed out of the pots. Harvested seeds sometimes required more than a year to germinate and more than once seedlings of *Meconella* appeared in flats or pots that had been abandoned the previous year for lack of productivity.

The pollen often is loose before the flowers open for the first time. For purposes of emasculating any of the species the small size of the buds makes it difficult to be certain that pollen has not already reached the stigmatic regions since some of the anthers are at about the same level as the base of the stigmatic surfaces. The stigmas expand in a day or so after anthesis and then the ovary elongates, lifting the stigmas above the anthers. No obvious pollinators have been observed in the wild state or in cultivation. A few interspecific crosses were attempted but none was successful. Some emasculated flowers prepared for cross pollinations produced a few viable seeds that later proved to be self-contaminants. In conjunction with the observation that fertile seeds apparently were produced at times when only a very few individuals of a species were in cultivation, it is suggested that the plants probably are at least partially self-compatible. The delay in the full expansion of the stigmas probably enhances the opportunity for outcrossing, especially when on bright days the petals and stamens are spread very broadly. Seed set seemed improved in flowers which had been rubbed with those of another plant. The flowers close at night through the duration of the petals, which may persist for a few days. It seems likely that there is ample opportunity for self-pollen to be deposited through purely mechanical means at least on the bases of the stigmatic regions without the intervention of insects. Occasionally, under the open conditions of the lathhouse, some fruits of all species aborted or did not produce seeds, suggesting the importance of outcrossing and/or pollinators. The most pertinent questions about the breeding behavior in Platystemonoideae cannot be answered at this time.

Size

Among the prominent variables is the size of the plant which may vary independently of the size of the flowers. Large and quite small plants frequently stand side by side in nature. The circumstances of crowding, the often substantial variation in seasonal rainfall or temperature, and the innate plasticity of the plants to respond, no doubt strongly affect the size of the flowers and of the plants beyond the generality that the last formed flowers are smaller than the first. No unusually large plants were recovered from wild seeds cultivated at Stanford although more or less giant plants occasionally occur in nature.

In a general way, the larger the organ the greater the amount of vasculature. Larger perianth segments usually have more veins than smaller ones. Smaller flowers in *Hesperomecon,* also may have fewer stamens (from many to as few as six); in *Platystemon* the larger flowers also may have more stamens as well as more carpels. The number of carpels in *Platystemon* is variable; in all others, with rare exception, the number of carpels is three. Generally *Platystemon* has the largest plants with the largest flowers, but in fringe areas such as some coastal strands and in drought the plants may be quite small with only a few leaves and flowers. Both *Platystemon* and *Hesperomecon* frequently occur in relatively rich grasslands where they must compete with other plants, especially in those seasons with ample rainfall. If climatic conditions are conducive to an unusually early and lush growth of introduced weeds and grasses, the plants of *Platystemon* and particularly *Hesperomecon* are likely to be overtopped and swamped. In drier years, *Platystemon* and *Hesperomecon* may flower above and slightly ahead of the other herbaceous vegetation. The frequency and conspicuousness of the plants in the same localities may vary from year to year.

Herbarium specimens indicate that before the complete urbanization of San Francisco moderate sized plants of both *Hesperomecon* and *Meconella californica* from this area had unusually large flowers. Across the Central Valley in the foothills of the Sierra of California, plants of both species seem to become progressively smaller from north to south. Size alone must be viewed as a treacherous taxonomic character.

Color

Color is a conspicuous variable in aerial portions of the plants. The petals of *Platystemon* often are described as cream-colored. In more extensive colonies of *Platystemon* some plants have bright yellow markings on the otherwise pale petals, and no two plants will seem to have the same pattern. The same is true for *Hesperomecon* and both sometimes have petals and/or sepals marginally tinged with reddish-purple. Information on the geographical distribution of color and patterns in terms of frequency of individuals exhibiting it should be freshly gathered since the color is lost on herbarium specimens.

Similar yellow color also is present in the petals of some plants of *Meconella californica* and a purplish tinge sometimes shows on the sepals. In this species the yellow occurs on the upper (adaxial) surface of the outer petals and the lower surface is quite pale. The flowers are striking with their bright yellow, broad outer petals and contrasting pale, narrower inner petals. This is the only example in the family of a truly two-colored corolla, and it is remarkable that the yellow color in this case is present by day but absent by night. This was confirmed over a period of three successive years at Stanford University with plants cultivated from seeds gathered in the western foothills of the Sierra Nevada of California. The color is present when the buds open for the first time but with the waning of the daylight in late afternoon and evening the color fades and in darkness the petals are white. By morning of the next day the bright color returns and this diurnal regeneration of the color continues in the same petals for a few days until the petals wither and fall. This color phenomenon, which reminds one of the presence and absence of scent, is analogus to other diurnal changes such as the opening and closing of flowers. The yellow color in the petals of *Platystemon* and *Hesperomecon* is similar but appears on both surfaces of the petals and is unaffected by light.

Not all plants of *Meconella californica* have yellow outer petals. The plants in the Coast Ranges only have white petals and plants with all-white petals also occur in the foothills of the Sierra so that this is not merely a difference between the plants of the eastern and western distributions. The two phases of *M. californica* are very similar morphologically but are strikingly distinct in regard to coloration; however, I do not feel that I can answer the question at this time as to whether these two phases should receive separate taxonomic recognition. The remaining two species of *Meconella* only have white petals, sometimes with an obscure greenish or yellowish spot immediately next to the attachment on the receptacle.

The color of the vegetative portions of the plants depends upon the presence of glaucousness, which is quite common, and also on the amount of pubescence, both of which are likely to be quite variable. There may be variation in the balance between yellow and green within the cells of the plant. Some of the plants of *Platystemon* with excessive, shaggy pubescence appear to be yellowish. The plants have a somewhat bitter taste, probably indicative of alkaloids. Under most circumstances the plants have a minute amount of thin, watery juice, but in a few instances a thick, golden orange sap, like that of many other Papaveraceae, was observed in some large and succulent plants of *Hesperomecon* and a whitish sap in *Platystemon*. Little importance can be attached to sap color as it has been found to be variable in other genera among similar plants.

Pubescence

Pubescence in *Platystemon* and *Hesperomecon* usually is conspicuous, particularly on the long peduncles, the sepals, and leaves. The fruits of *Hesperomecon* are glabrous, but those of *Platystemon* sometimes have prominent, stiff, upwardly curving hairs. The amount of pubescence is difficult to quantify. It seems somewhat more constant but less abundant in *Hesperomecon*. From time to time excessively shaggy plants of *Platystemon* are found and, less frequently, very sparsely hairy plants. Both *Hesperomecon* and *Platystemon* contrast markedly in this respect with *Meconella* which is glabrous or with a few short warty hairs only on the apex of the sepals. In all cases the hairs are multicellular and multiseriate. If the cells lie parallel the hair appears smooth, but if the upper tips of the cells turn outward, the hair appears rough. Rough and smooth hairs often occur on the same plants. Unbranched multiseriate hairs also characterize subfamily Papaveroideae, but the hairs of subfamily Chelidonioideae are uniseriate or branched. The hairs of Eschscholzioideae are unicellular. Glabrous plants, of course, occur in all groups. The amount of pubescence as a taxonomic character is unreliable throughout the family; however, the cellular composition of the hairs is a useful criterion for establishing higher taxa in Papaveraceae.

Cytology

The chromosomes of *Platystemon*, n=6, and *Hesperomecon*, n=7, are relatively large and easily studied (Figs. 6, 7). Supernumerary chromosomes have been observed in *Platystemon californicus*. Multivalents are unusual features of *Hesperomecon linearis*. The chromosome number for *H. linearis* was reported earlier (Ernst, 1958) under the name of *Meconella linearis*. Persistent nucleoli seem to be frequent in both *Meconella* and *Hesperomecon*. No obvious multivalents have been seen in *Meconella* although some examples of possible secondary attraction between bivalents has been noted.

The chromosome number for each of the three species of *Meconella* is n=8 (Fig. 7). Supernumerary chromosomes and multivalents also have been observed in *Canbya*. The chromosomes of *Meconella* seem smaller and more difficult to study than those of either *Platystemon* or *Hesperomecon,* and the chromosomes of *M. oregana* are the smallest of all (Fig. 7T). The morphology of the chromosomes within taxa appears to be somewhat variable and these peculiarities should serve as useful markers in studies of cytological races.

Genomes of six or seven pairs of chromosomes (and multiples or other numbers) are found in Papaveroideae and Eschscholzioideae, and six pairs (and other numbers) in Chelidonioideae. Eight pairs of chromosomes, as in *Meconella,* are unusual in Papaveraceae, being known only in *Meconopsis (Cathcartia) villosa* and *Canbya* (here complicated by supernumerary chromosomes) but are somewhat more common in Fumariaceae.

Floral Morphology

The peduncle and perianth. The bundles in the peduncles coalesce apically to form a cylinder of trachreary tissues, here called the receptacle framework, which frequently is interrupted by irregular gaps. The peduncles of *Platystemon* and *Hesperomecon* contain six vascular bundles and each is directly below a segment of the perianth (Fig. 4). Three lead directly to the sepals and the alternate three directly to the outer series of petals. While each of the sepals of *Platystemon* has three main traces, each trace divides below the articulation of the sepal on the surface of the receptacle. The lateral traces to adjacent sepals are branches from a common trunk. Each of the petals also has three main traces which also divide before reaching the base of the petal. The three main traces to a petal all originate from a single trunk, but the three main traces to the sepals represent three different trunks. Each petal trunk is directly associated with a sepal trunk, and the two emerge jointly from the receptacle framework directly over a bundle in the peduncle. The internal features of the perianth in *Hesperomecon* are very similar to those of *Platystemon* with only a little less branching of the traces before they enter the bases of the appendages. An alternative explanation of the vascular pattern of the perianth is that each petal has a single basic trace (which branches and looks like three traces) while a sepal has three basic traces (which also branch). It is very difficult to standardize the numerical references for petal traces since some petals, e.g., in some species of *Eschscholzia* and *Meconopsis*, clearly have multiple traces. Three traces to the petals seems to describe *Platystemon* and *Hesperomecon,* but in *Meconella denticulata,* because of the relative depth of the receptacle, a petal would seem better described as receiving a single trace.

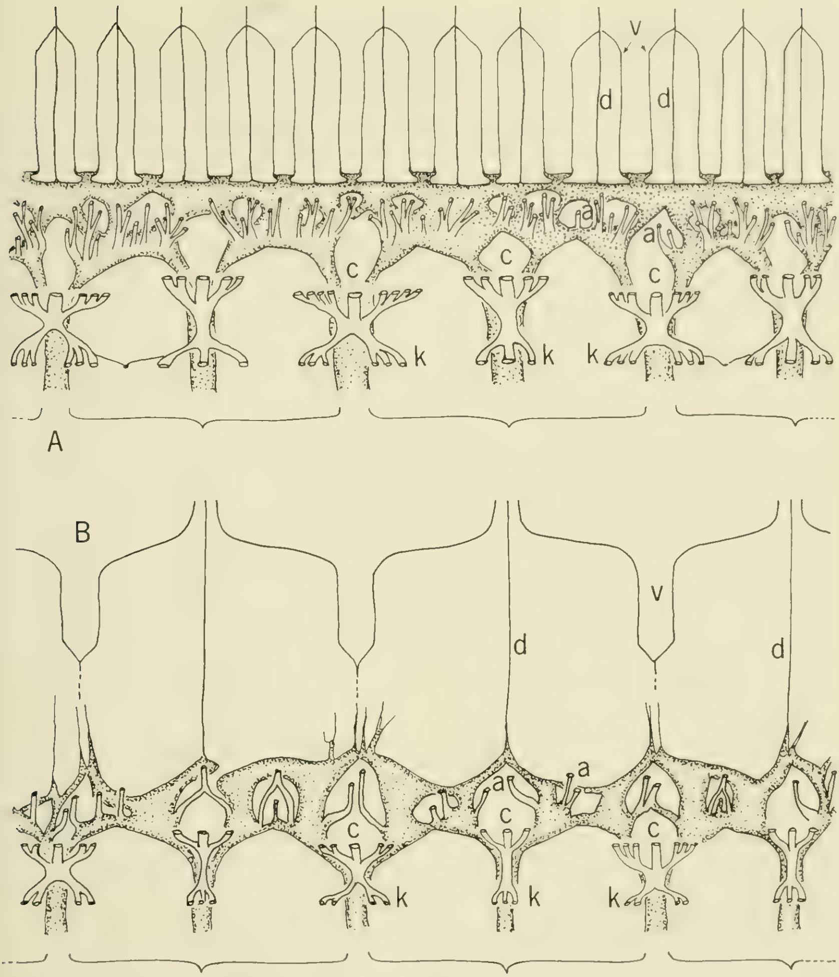


FIG. 4. Vertical diagrams of vascular patterns in cleared flowers. —A, *Platystemon californicus, Ernst 108*; diameter of receptacle ca 2 mm. —B, *Hesperomecon linearis, Ernst 214*; diameter of receptacle ca 1.5 mm. —a, stamen traces; c, petal traces; d, dorsal bundles; k, sepal traces; v, free ventral bundles of carpels; horizontal brackets enclose sepals.

There only are three bundles in the peduncles of *Meconella* (Fig. 9A, D, G). The bundles that are lost are the ones that would alternate with the sepals, i.e., those directly below the superposed placental regions, the outer petals, and the lateral traces to the sepals. There are lateral traces to the sepals in *M. denticulata* so that each sepal is well vascularized with the branches from three main traces. The lateral traces to the sepals are deleted in *M. californica* and *M. oregana;* thus, the sepals receive only a single trace which usually remains unbranched.

The gathering together of the tracheary threads first into a fascicle of petal traces and of sepal traces, and these joined ultimately into a common trunk on the receptacle framework, may not be quite correct from the ontogenetic point of view but this describes the end pattern of the perianth. For petal traces to be intimately associated with sepal traces is common; however, the pattern exemplified in Platystemonoideae and *Canbya* (Fig. 11D) seems, by comparison to other Papaveraceae, to be both simple and compact and to represent a high degree of organization. Relative advancement especially is evident in *Meconella* with its reduction in number of bundles in the peduncle, and reduction in amount of vasculature to the sepals and petals.

The androecium. The insertion of the stamens in Papaveraceae is diverse. In most species with relatively large flowers and indefinite number of stamens, the traces to the stamens are gathered into fascicles or some kind of complicated internal branching system. In *Dendromecon,* a woody genus of Eschscholziodideae, it is notable that the traces to individual stamens are double and seem to be arranged in more or less vertical series. In both *Hesperomecon* and *Platystemon* there normally are many stamens which more or less are uniformly distributed around the periphery of the receptacle (Fig. 4). The stamens in *Platystemon* sometimes are claimed to be spirally arranged, but the traces to the stamens seem to be inserted at random and are not in any particular order since they originate both singly and in clusters on a receptacle framework which also is interrupted by gaps. In this instance the pattern would seem better described as resulting from the crowding of the maximum number of stamens into the available space on the surface of the receptacle. The extent of truly spiral arrangement of floral appendages and its significance requires further investigation. There are other examples in Papaveraceae, i.e., *Meconopsis,* where the stamens superficially may appear to be spirally arranged, but internally the staminal traces are associated with very elaborate branching systems which are not spirally oriented.

There are only six or fewer stamens in *Meconella denticulata* and *M. oregana,* inserted more or less alternately with the petals in a single series. The stamens in *M. californica* are unequal in length and are inserted in two cycles with a total of about 12 stamens (Fig. 9). The outer stamens are somewhat shorter and alternate with the petals; the inner ones are opposite the petals. Reduction in the number of stamens is to be expected in the southern regions of distribution in *M. californica* and also in *Hesperomecon.* Smaller flowers in any case can be expected to have fewer stamens than larger ones.

The morphology of the filaments often is variable within a species and within a flower. The filament frequently is expanded laterally and apically dilated or sometimes toothed. The anthers contain four chambers of pollen mother cells and become two-locular at anthesis. The anthers in *Platystemon, Hesperomecon,* and *Meconella denticulata* (Figs. 5B; 8D; 9B) are distinctly

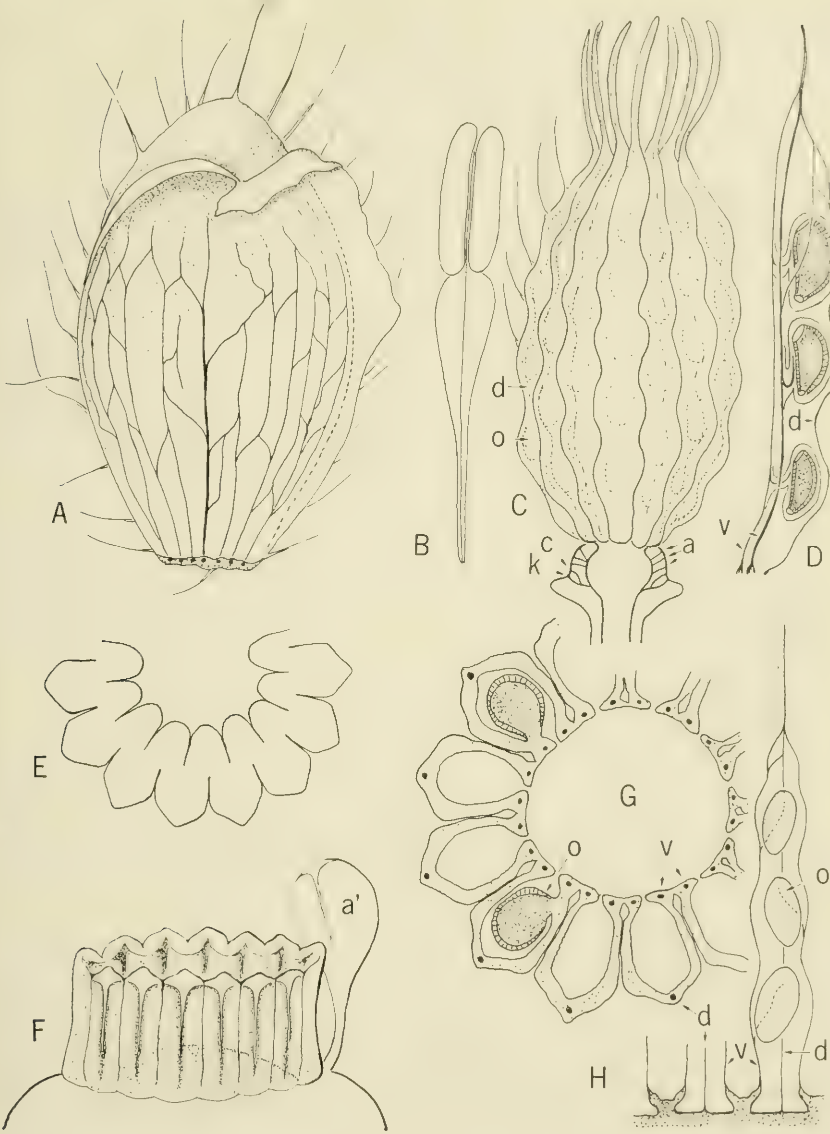


FIG. 5. Diagrams of floral appendages of *Platystemon californicus, Ernst 108.* —A, sepal, adaxial view, X 8; B, stamen, adaxial, X 9; C, cleared ovary shown as though partially transparent over longitudinal section of receptacle, X 9; D, carpel showing attachment of ovules, X 7; E, young gynoecium viewed from above showing lateral continuity of carpels, X 56; vertical view of E with one stamen, shown as though transparent, the domed floor and the thick placental regions darkened, X 56; G, transverse section through ovary showing position of locules and ovules around a central cavity, X 20; H, traces to carpels showing attachment of ovules and position of dorsal and ventral bundles. X 7. —a, stamen traces; a′, stamen; c, petal traces; d, dorsal bundles; k, sepal traces; o, ovules; v, ventral bundles.

oblong but those of *M. californica* and *M. oregana* (Fig. 9E, H) are orbiculate to ovoid or deltoid. The anthers of *M. denticulata* frequently are as long or longer than their filaments. The pollen is tricolpate in all species.

The gynoecium. The gynoecia of Papaveraceae are syncarpous and composed of two to many carpels and, for the most part, the stigmas are united or continuous from carpel to carpel by some kind of stylar union or by duplex commissural development of the stigmas. Most of the family also have intracarpellary valves by means of which the seeds are dispersed from the fruits (Fig. 11). The Platystemonoideae have three carpels except in *Platystemon* where there are several to many carpels; in all cases valves are lacking and the stigmas are free. More than one gynoecium occasionally develops in a flower of *Platystemon* resulting in two or more adjacent independent whorls of carpels (see Jepson, 1922, p. 555). The morphology of the gynoecia in *Platystemon, Hesperomecon* (as *Platystigma*), and *Meconella* was described clearly by Lignier (1911) and subsequently by others, most of whom saw and illustrated essentially the same structure.

A morphological explanation of the carpel perhaps still is debatable, but the conception of solid and open carpels discussed by Eames (1961, pp. 197, ff) is no more enlightening than the earlier hypothesis of carpel polymorphism of Saunders (1937) which it attempts to replace and both seem unnecessarily elaborate for Papaveraceae. The more traditional Candollean interpretation provides the best working hypothesis for all Papaveraceae, and it is essential for the examples in *Platystemonoideae* which have free stigmas and as many carpels as stigmas.

When the primordium of the gynoecium of *Platystemon* first is evident on the floral meristem, it is a continuous, low, circular crest with undulating margins both apically and laterally. Soon this structure somewhat resembles the flutings on an old fashioned handmade pie shell (Fig. 5E, F). In the horizontal plane the outer (abaxial) convexities become the dorsal regions of the carpels; the inner (adaxial) convexities are the fused ventral margins of the carpels (duplex placentae), and the indentations between them become the locules. The developing carpels with their intruding placentae and the indentations of their as yet undefined locules surround the open central chamber of the gynoecium with its domed floor. In the vertical plane the high parts of the undulations become the stigmatic lobes and the low ones the placental regions.

From an ontogenetic viewpoint, the gynoecia of the five species of Platystemonoideae, disregarding the greater number of carpels in *Platystemon,* differentiate on the floral meristem into much the same original form. There is complete continuity of the tissues from carpel to carpel around an open central chamber into which each of the theoretically duplex future placental regions intrudes. Alternating with the placentae are centrifugal outpocket-

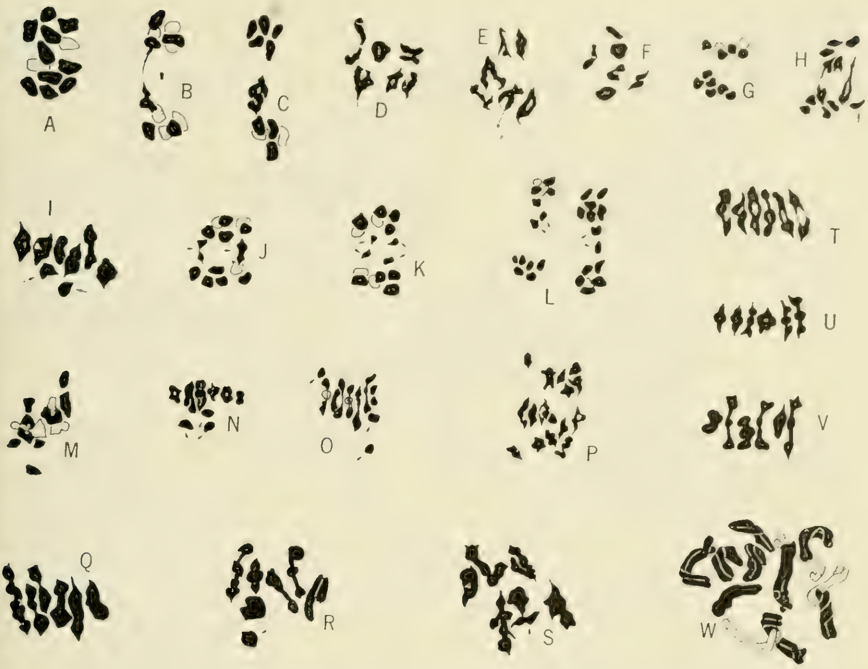


Fig. 6. Pollen mother cell chromosomes of *Platystemon californicus*, first division A-V except L, second division; W, premeiotic mitosis in anther. —A-C, *Ernst 103:* A, 6+6 chromosomes at anaphase I; B, bridge and fragment; C, delayed separation of 1 bivalent. —D-H, *Ernst 108:* D, E, F, 6 bivalents; G, 6+6 at AI; H, delayed separation of 2 bivalents plus 1 supernumerary. —I-L, *Ernst 164:* I, 6 bivalents plus 2 supernumeraries; J, K, 6+6 and supernumeraries at AI showing division of 2 supernumeraries; L, showing supernumeraries at second telophase. —M to S, examples of irregular divisions with supernumeraries. M-P, *Ernst 111;* —Q—S, *Ernst 176:* —T-V, each showing 6 bivalents: T, *Ernst 234*; U, *Ernst 491*; V, *Ernst 515.* —W, *Raven 15213:* showing 12 somatic chromosomes. —Arrows indicate some of the supernumerary chromosomes.

ings of the central chamber in the position of each of the dorsal trace regions of the carpels. When viewed in the transparent condition, the ovary wall has alternating thick and thin regions in transverse section (Fig. 8H-J). In *Meconella* and *Hesperomecon,* development leads to a gynoecium of three parietal placentae around a single central locule and the thickness in the placental regions diminishes.

Unlike the gynoecium of *Hesperomecon,* which is deformed into a three-cusped shape in transverse section with diffuse placental regions, the gynoecia of the three species of *Meconella* remain essentially round in transverse outline and the placental regions are vertically restricted (Fig. 8F, G). The ovary wall in *Platystemon,* however, appears peculiarly abaxially deformed in such a way that the several intrusive placentae continue to jut into the original central chamber while at the same time the outpocketings of the central cham-

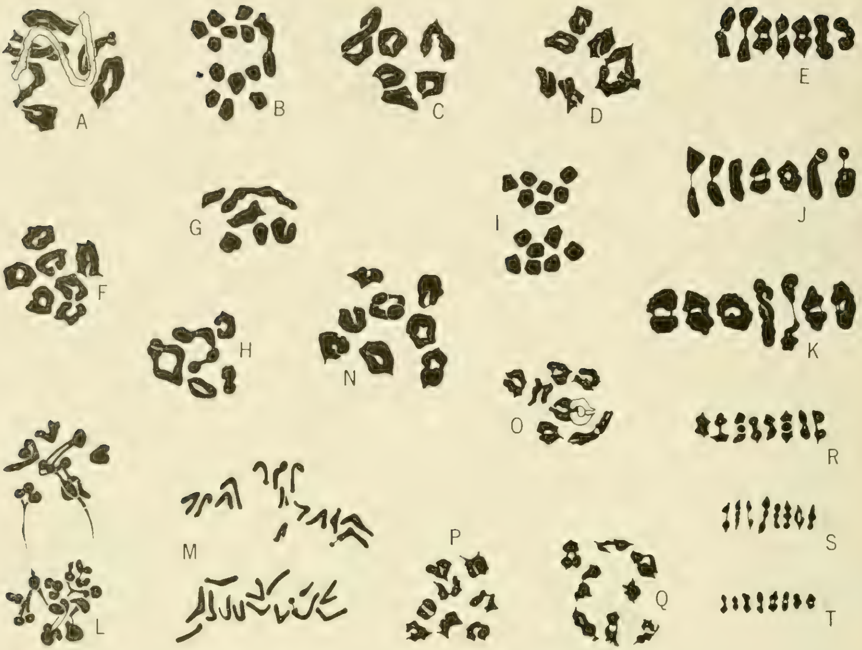


FIG. 7. Pollen mother cell chromosomes of *Hesperomecon linearis,* A-L; M, premeiotic mitosis in anther. *Meconella,* N-T. —A, B, E, *Ernst 235a:* A, 7 bivalents; B, delayed separation of bivalent with ?fragment; E, 7 bivalents. —C, D, F, *Ernst 235b:* C, D, 5 bivalents plus 1 tetravalent and nucleoli; F, 7 bivalents. —G-I, *Ernst 235c:* G, 5 bivalents plus 1 tetravalent; H, 3 bivalents plus 2 tetravalents; I, 7+7 at anaphase I. —J, K, L, *Lewis s.n.:* J, K, 7 bivalents; L, bridges at anaphase I. —M, *Ernst s.n.:* 14+14 somatic chromosomes at anaphase showing satellites. —N-P, *M. denticulata:* N, *Ernst 160,* 8 bivalents; O, *Ernst 158,* 6 bivalents plus ?tetravalent; P, *Ernst 158,* 8 bivalents and nucleolus. —Q, R, S, *M. californica:* Q, *Ernst 230,* 8 bivalents and nucleolus; R, *Ernst 210,* 8 bivalents; S, *Ernst 214,* 8 bivalents. —T, *M. oregana, Ernst 243,* 8 bivalents.

ber enlarge and become enclosed by what amounts to a kind of conduplication of the carpels (Fig. 5G). This leaves all of the duplex placentae in close proximity adaxially and the outpockets are pinched off from the central chamber as lateral locules. The lateral margins of adjacent carpels, of course, are fused from the beginning in this syncarpous gynoecium. Later development of the gynoecium, which intensifies the peculiar folded aspect of the ovary wall, causes self-margins of the respective carpels to be closely appressed internally but they do not unite. The conspicuous characteristics of the gynoecium of *Platystemon* have led botanists to consider it to be essentially apocarpous. These characteristics are superficial features of later rather than of earlier ontogeny and seem like exageration of the same basic development which in *Hesperomecon* and *Meconella* only can be interpreted as genuinely syncarpous.

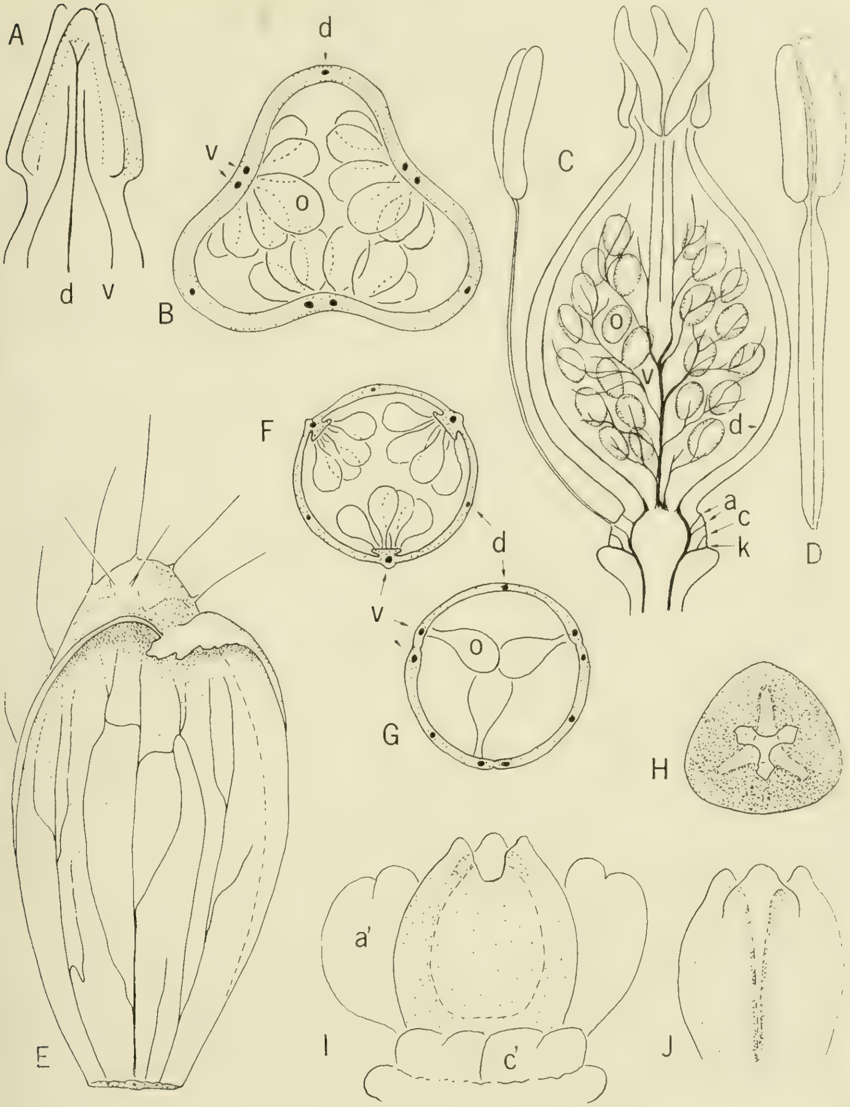


FIG. 8. Diagrams of floral appendages of *Hesperomecon linearis, Ernst 214,* A-E; and of *Meconella,* F-J. —A, vasculature of stigma showing apical bifurcation of dorsal bundle, X 15; B, transverse section of ovary showing ovules and major vascular bundles, X 20; C, ovary shown as though transparent over longitudinal section of receptacle, and lateral view of stamen, X 13; D, adaxial view of stamen, X 13; E, adaxial view of sepal, X 12. —F, transverse section through ovary, *M. denticulata, Ernst 158,* X 27. —G, transverse section through ovary *M. californica, Ernst 215,* X 27. —H, I, J, *M. oregana, Ernst 252: H,* cleared view of I and J from above, X 100; I, meristematic ovary shown as though transparent, view through placental region, thicker portions darkened, X 100; J, vertical view of 1 turned through 90°, observed through dorsal region. —a, stamen trace; a′, stamen; c, petal traces; c′, petal; d, dorsal bundles; k, sepal traces; o, ovules; v, ventral bundles.

By the time that the pollen mother cells have divided, the lateral margins of the several carpels in *Platystemon* are marked by deep external depressions. The ovules are attached alternately to the opposing internal margins of their respective carpels in a single vertical series. Transverse sections of the ovary embedded in paraffin taken as late as the pollen tetrad stage in the inner anthers, which still is before the formation of the embryo sacs, clearly demonstrate the continuity of the epidermal and parenchymatous tissues from carpel to carpel in *Platystemon*.

The development of the dorsal bundle in the carpel is of interest. In *Platystemon* and *Hesperomecon*, the dorsals are well developed, differentiating upward from the bases of the carpels to the tips of the stigmas. The dorsals have been observed to reach the stigmatic lobes in *Platystemon* long before the ventrals were visable. In *Meconella*, however, the dorsals are delayed and it is the ventrals that reach the stigmas first. The dorsal usually extends to the stigmas in *M. denticulata*, but in *M. californica* and in *M. oregana*, it frequently is incomplete, stopping before reaching the stigma (Fig. 9A, D, G). The dorsal sometimes was absent in materials of both species when studied as late as the time of anthesis. Examination of the fruits on herbarium specimens, however, shows that the dorsal sometimes is completed and that the delayed development must be observed in younger ovaries.

The dorsals in Chelidonioideae and Eschscholzioideae normally are strong and complete, but in Papaveroideae they frequently are vestigial (as in *Canbya*, Fig. 11), absent (as in *Argemone*), and sometimes (as in *Papaver* and *Roemeria*) are replaced by strong pseudodorsal bundles which originate from the placental bundles. Reduction of the dorsal bundle, its complete absence, and particularly, its replacement by a pseudodorsal, certainly provides insight into the evolutionary advancement of the carpel in these taxa, but, obviously, it is not possible to erect a phylogeny for these plants merely on this basis and to the exclusion of other morphological phenomena.

The placental regions of the ovary in *Meconella denticulata* contain a single strong placental bundle which, near the apex, divides, sending a branch to the stigmatic lobe on either side (Fig. 9A). In *Hesperomecon*, there is a fascicle of traces toward the bottom in the ventral position, a more or less strong, single placental bundle through the lower portion of the ovary, but toward the top the placental bundle divides into a pair of veins which pass to the stigma on either side (Figs. 4B; 8B, C). Each placental region in *Platystemon* has a pair of ventrals, but these are joined basally at their point of insertion on the receptacle framework (Figs. 4A; 5G, H). In transverse section each carpel appears to be folded inwardly (ventrally conduplicate) so that the margins oppose one another. The duplex nature of the placental regions (which are the fused margins of adjacent carpels) is emphasized by the paired (as well as seemingly inverted) ventral bundles in transverse section (see Arber 1938, pp. 662, 663; Lignier 1911).

The placental regions in *Meconella californica* and *M. oregana* contain a pair of veins from bottom to top (Figs. 9D, G; 8G). It is notable that the ventral veins of a given carpel in these two species arise very near to their dorsal on the receptacle framework which strongly enhances the apocarpous-like appearance of the vasculature because the vasculature of each carpel is totally independent of the others. The adjacent ventrals of adjacent carpels in *Platystemon* actually are inserted closer to one another than they are to their respective dorsal and they are joined basally (Figs. 4A; 5D, G, H). In *Hesperomecon* and *M. denticulata* the ventrals of adjacent carpels clearly are united (Figs. 4B; 8C; 9A). Subsequent connecting veins between dorsal and respective ventrals are established in all species.

The fruit cleaves at maturity through the placental region so that whole carpels separate partially or completely. In *Platystemon, Meconella californica,* and *M. oregana,* the line of cleavage passes through the placental region between the paired ventrals of adjacent carpels. In *M. denticulata* and *Hesperomecon* the cleavage is the same in the apical portion, but below this there is a single placental bundle rather than a pair of ventrals. Separation of the carpels is arrested by the bundle or the bundle must be torn free from one or the other of the adjacent carpels. The ovary wall closely invests the seeds in *Platystemon* and the carpels finally fragment into one-seeded segments. The seeds in the fruits of other species of Platystemonoideae are loose.

The dehiscence of fruits in other Papaveraceae is exemplified by *Canbya* (Fig. 11). The stigmas in *Canbya* are permanently united into a stigmatic mechanism with elaborately developed commissural appendages, and each of the placental regions contains a single well developed placental bundle. Valves are formed in the ovary wall between the placental bundles. The valves open basipetally in subfamily Papaveroideae, creating a pore toward the top of each carpel through which the seeds are liberated. The placental bundles and the stigmatic mechanism are persistent and remain united. The seeds are dispersed, in this case, through intracarpellary valves in the fruit wall whereas in subfamily Platystemonoideae seeds are scattered by the disassociation of whole carpels.

A few points can be assembled to summarize this discussion of the gynoecium. The terms apocarpous and syncarpous normally describe totally different morphological conceptions. The Papaveraceae are syncarpous but the contrast between apocarpous and syncarpous in terms of the vascular supply to the carpels becomes somewhat ambiguous in the Platystemonoideae. The gynoecia of all Platystemonoideae, in all cases, clearly are syncarpous ontogenetically with complete continuity of the non-vascular tissues from carpel to carpel. The vascular patterns in both *Meconella denticulata* and

Hesperomecon are so conventional as not to require comment, but the vasculature in the other three taxa, i.e., *M. californica, M. oregana,* and *Platystemon,* somewhat resembles apocarpous patterns. The apocarpouslike con-

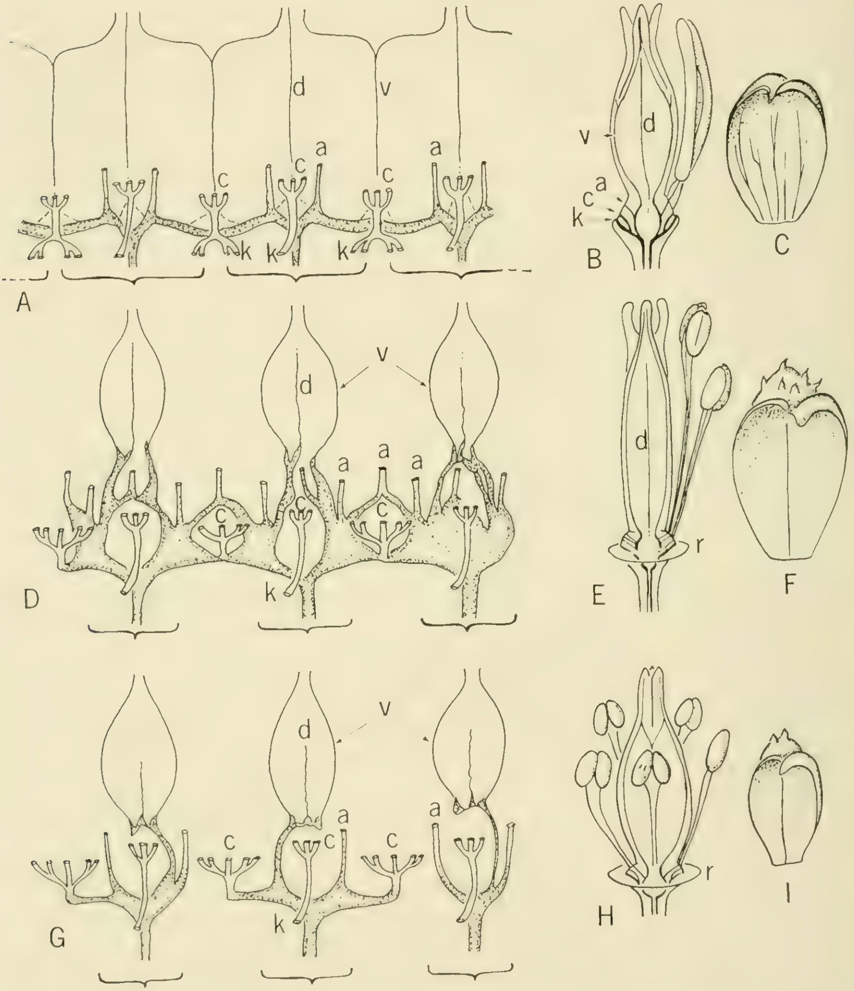


FIG. 9. Diagrams of vascular patterns and appendages in flowers of *Meconella.* —A-C, *M. denticulata, Ernst 158:* A, vertical diagram of receptacle, diameter of receptacle ca 0.5 mm; B, cleared ovary on longitudinal section of receptacle showing 1 stamen, X 13; C, adaxial view of sepal showing venation, X 8. —D-F, *M. californica, Ernst 215:* D, vertical diagram of receptacle, diameter of receptacle ca 1 mm; E, cleared ovary on optical section of receptacle showing two unequal stamens and receptacle rim, X 9; F, adaxial view of sepal showing single vein, X 8. —G-I, *M. oregana, Ernst 252:* G, diameter of receptacle ca 0.5 mm; H, cleared ovary on optical section of receptacle showing stamens and receptacle rim, X 13; I, adaxial view of sepal showing single vein, X 10. —a, stamen traces; c, petal traces; d, dorsal bundles; k, sepal traces; r, receptacle rim; v, placental or ventral bundles.

dition of the vasculature in *M. californica* and *M. oregana* is inconspicuous externally although internally it is more strikingly developed than in *Platystemon* which previously has been considered essentially apocarpous on the grounds of its external appearance.

DISCUSSION

A glance at the floral diagrams (Figs. 4, 9) suggests a simple evolutionary reduction series such as from *Platystemon*→*Hesperomecon*→*Meconella denticulata*→*M. californica*→to *M. oregana.* An increase in chromosome number from *Platystemon* to *Hesperomecon* is accompanied by a reduction in the number of carpels and stamens but this relationship will be reconsidered shortly. From *Hesperomecon* to *Meconella* there is a reduction from six to three bundles in the peduncles, a reduction in number of stamens as well as a change in arrangement from indefinite to definite and cyclic, and an increase in chromosome number. More important, perhaps, are the modifications in *M. californica* and *M. oregana,* including a reduction in vascularization of the perianth, particularly in the sepals; a tendency for late appearance and incomplete development of the dorsal bundle of the carpels; and spatial separation of the vascular supply of the carpels which increases the apocarpouslike structure of the gynoecium. The double cycle of stamens in *M. californica* might be a simple multiplication of parts in an otherwise diminishing sequence. In *M. oregana* there is an increase in the frequency of teretological fusions, additions and deletions.

The reduction series from *Hesperomecon* through *Meconella oregana* seems clear and well preserved in contemporary plants. The highly reduced *M. oregana,* probably one of the most highly advanced species of Papaveraceae, culminates a tendency for loss of parts in peduncle, perianth, androecium, and gynoecium. The most interesting aspect of this morphological sequence is the development of the strongly, although concealed, apocarpouslike vascular supply of the gynoecium, apparently through reduction within a typically syncarpous family accompanied by the simultaneous deterioration of the dorsal trace.

The five species of Platystemonoideae, after consideration of many aspects of the plants, seem to conform to a linear sequence, i.e., *Platystemon, Hesperomecon, Meconella denticulata, M. californica,* and *M. oregana* (Fig. 10). The distinctive spatulate leaves clearly separate the species of *Meconella.* The remainder of the arrangement is influenced by a few structural features of the carpels and the reduction-multiplication series in vascular supply in the flowers. The relationship of *Platystemon* and *Hesperomecon* to the three species of *Meconella* seems well established. The individual position of the three species of *Meconella* is less exactly fixed since there are not a large number of characters for consideration; however, *M. californica* and *M.*

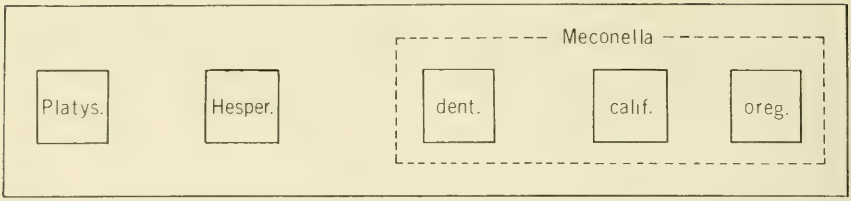


FIG. 10. Intuitive linear arrangement of the five species of Platystemonoideae based upon estimated phenotypic and morphological similarities.

organa must be adjacent, and it is clear that *M. denticulata* stands somewhat apart. On external features *M. denticulata* and *M. oregana* are phenotypically close, but internally they are more remote on the basis of presence of receptacle rim, relative length to width of receptacle, length of anther to filament, and the distributional disjunction. It could be argued that phenotypically *M. californica* with its more numerous stamens and sometimes colored petals should receive a position closer to *Hesperomecon.* Alternative arrangement of the species is possible, but I believe that a linear one as presented above is the most representative of the relationship. In this system, the direction of diminishing complexity of floral structure clearly is from left to right. The size of the flowers usually is largest in *Platystemon* and smallest in *M. oregana,* and generally the amount of vascularization varies more or less directly with the size of the flower or organ in Papaveraceae. This sequence, when read from left to right, also reflects the increased localization of the plants to more mesic sites and the increase in number of chromosomes.

It is tempting also to read this morphological series from left to right as the phylogenetic history of these species. I hesitate to accept this as a phlogeny in the historical sense because, morphologically, the sequence reads just as well in the opposite direction and, phylogenetically, we are left without a reliable corner stone. Reading from left to right is more appealing because it places *M. oregana* with its reduced dorsal bundle in the carpel, along with general diminution of floral structure and size, in the most derived position. If it merely is the apocarpouslike structure *per se* of *Platystemon* which causes it to be thought of as a prototype, then *M. oregana* with its even greater apocarpouslike structure, is just as likely a protoype. If either extreme, i.e., *Platystemon* or *M. oregana,* is the prototype and if this sequence is phylogenetic, then apocarpouslike plants at one end have generated typically syncarpous plants in the middle only to revert once again to producing apocarpouslike plants at the far end.

The morphology of either *Platystemon* or *M. oregana* seems too queer for a direct comparison with other Papaveraceae under the circumstances of this discussion. The morphology of *Hesperomecon* is more general and, perhaps, in the abstract sense, it might require the least amount of modification to be even more nearly like other Papaveraceae. While it is speculative, I could readily believe that *Hesperomecon* is a kind of model on which evolution may have pivoted, giving rise through a reduction series leading to the apocarpouslike structure of *M. oregana,* on the one hand, and to the rather different apocarpouslike structure of *Platystemon,* on the other. As an abstraction, this scheme seems the most reasonable means to explain the evolution of form but it relies too heavily upon the symbolism that some living species are directly derived from other contemporary species.

The basic taxonomic units of Platystemonoideae already are known, and their general similarities should be evident from the foregoing discussion. The first of two objectives now is to compare these similarities by some impartial method. The second objective is to attempt to interpret the similarities phylogenetically. Computer methods provide the appropriate techniques for the first purpose.

Table 1 introduces 18 morphological characters having two different states which are coded by the numerals 1 and 2. A cytological character is added which has three states. All characters have been discussed in the preceding text.

Table 2 presents a matrix showing the coded state of each character for each species. This table also indicates the mean and the standard deviation for each character. From these data the character states were standardized and the Mean Character Difference, the Taxonomic Distance, and the Correlation Coefficients were calculated by H. J. Thompson and A. J. Hill, following the methods of Sokal & Sneath (1963), and using the Engineering Computing Facility at the University of California at Los Angeles. The details of these calculations could be supplied to interested readers.

Table 3 shows the Mean Character Differences (MCD) matrix in which the lowest value (0) indicates the lowest difference, i.e., the closest similarity. These data were the basis for the comparisons shown in the five-sided figure of Table 4C and for the dendrogram shown in Table 4B.

The rounded-off Mean Character Difference values (Table 4C) indicate that *Meconella californica* and *M. oregana* must be adjacent and that *M. denticulata* clusters with them as shown in the dendrogram (Table 4B). It is also evident that *Hesperomecon* and *Platystemon* must be adjacent and that the next closest affinity is between *Hesperomecon* and *M. denticulata.* This lends credibility to the order of the names on the dendrogram (Table 4B) for *Platystemon, Hesperomecon,* and *Meconella denticulata* and for Fig. 10. Table 4C shows that *M. oregana* is equidistant from both *Platystemon* and *Hesperomecon;* also that *M. californica* is equidistant from both *Platystemon* and *Hesperomecon* although slightly closer to them. The values in the five-sided figure (Table 4C) demonstrate that the spatial relationships

TABLE 1. Characters that show different states in the five species of Platystemonoideae and their codes. All are two-state characters except the last which is three-state.

Characters	State	Code
1.	Plants pubescent	1
	Plants glabrous	2
2.	Shoots elongating	1
	Shoots not elongating	2
3.	Leaves linear	1
	Leaves spatulate	2
4.	Peduncle bundles six	1
	Peduncle bundles three	2
5.	Receptacle rim minute	1
	Receptacle rim absent	2
6.	Sepal traces one	1
	Sepal traces three	2
7.	Petals only white	1
	Petals sometimes yellow	2
8.	Stamens many, indefinite	1
	Stamens few, definite	2
9.	Stamens single series, equal	1
	Stamens more than one series, and unequal	2
10.	Anthers long	1
	Anthers short	2
11.	Carpels three	1
	Carpels more	2
12.	Dorsal carpel trace well developed	1
	Dorsal carpel trace vestigial or incomplete	2
13.	Ventrals of carpels separate	1
	Ventrals of carpels united	2
14.	Ovules in single vertical series	1
	Ovules in more than a single series	2
15.	Fruit elongating, twisted	1
	Fruit not elongating, not twisted	2
16.	Stigma short	1
	Stigma long	2
17.	Ovary not fragmenting transversely, seeds free	1
	Ovary fragmenting transversely, seeds not free	2
18.	Ovary wall deformed	1
	Ovary wall circular	2
19.	Chromosome number six	1
	Chromosome number seven	2
	Chromosome number eight	3

among the five species, if precisely plotted, would describe a peculiar three-dimensional polygon rather than the straight line shown in Fig. 10. Not supported is my contention that *M. denticulata* stands at least as far removed from *M. oregana* as from *M. californica*. This contrasts the freedom of thought allowed in an intuitive method with the rigorous limitations imposed by the precision of computer techniques.

The dendrogram (Table 4B) is redrawn from a printout obtained from the Mean Character Difference matrix of Table 3 by the method of clustering

TABLE 2. Data matrix with mean and standard deviation for the five species of Platystemonoideae coded from Table 1.

OTU Char.	*Platys.*	*Hesper.*	*M. dent.*	*M. calif.*	*M. oreg.*	MEAN	ST. DEV.
1.	1.000	1.000	2.000	2.000	2.000	1.600	0.548
2.	1.000	2.000	1.000	1.000	1.000	1.200	0.447
3.	1.000	1.000	2.000	2.000	2.000	1.600	0.548
4.	1.000	1.000	2.000	2.000	2.000	1.600	0.548
5.	1.000	2.000	2.000	1.000	1.000	1.400	0.548
6.	2.000	2.000	2.000	1.000	1.000	1.600	0.548
7.	2.000	2.000	1.000	2.000	1.000	1.600	0.548
8.	1.000	1.000	2.000	2.000	2.000	1.600	0.548
9.	2.000	2.000	1.000	2.000	1.000	1.600	0.548
10.	1.000	1.000	1.000	2.000	2.000	1.400	0.548
11.	2.000	1.000	1.000	1.000	1.000	1.200	0.447
12.	1.000	1.000	1.000	2.000	2.000	1.400	0.548
13.	1.000	2.000	2.000	1.000	1.000	1.400	0.548
14.	1.000	2.000	2.000	1.000	1.000	1.400	0.548
15.	2.000	2.000	1.000	1.000	1.000	1.400	0.548
16.	2.000	1.000	1.000	1.000	1.000	1.200	0.447
17.	2.000	1.000	1.000	1.000	1.000	1.200	0.447
18.	1.000	1.000	2.000	2.000	2.000	1.600	0.548
19.	1.000	2.000	3.000	3.000	3.000	2.400	0.894

by weighted pair-groups (Sokal & Sneath, 1963). The MCD values are shown at the left of the dendrogram and by the solid horizontal bars. In actual practice the data of Table 3 were inverted for convenience of the operation. The arrangement of names of the taxa at the top of the dendrogram is according to my preference, a value judgment, but is supported in part by the relationship exhibited by the five-sided figure of Table 4C. A similar dendrogram was obtained from the Taxonomic Distance matrix which was calculated from the standardized character values (not shown). The two dendrograms were nearly identical in appearance but their vertical scales were different and do not have a clear relationship. The clustering in the two dendrograms was the same and in the same order. The dendrogram obtained from the Correlation Coefficients matrix also agreed in general with the Mean Character Difference dendrogram.

The dendrogram obtained by computer methods (Table 4B) is similar to that obtained from a simple matching analysis of the characters listed in Table 1. The coding of the characters in Table 2 is the data for Table 4A.

TABLE 3. Similarity matrix of Mean Character Difference for the five species of Platystemonoideae, calculated from Table 2.

OTU	*Platys.*	*Hesper.*	*M. dent.*	*M. calif.*	*M. oreg.*
Platys.	0.	0.818	1.528	1.336	1.528
Hesper.	0.818	0.	0.945	1.330	1.522
M. dent.	1.528	0.945	0.	0.769	0.577
M. calif.	1.336	1.330	0.769	0.	0.192
M. oreg.	1.528	1.522	0.577	0.192	0.

All matching characters between any two possible combinations of species was tallied; thus, each time a character state was the same for any two species it was counted. The values in the lower left of Table 4A represent the sums of matching character states for each pair of species. The values in the upper right are equivalents expressed in percent. For convenience 20 rather than 19 was selected for the denominator in computing percent.

The values in Table 4A could be inserted into the appropriate places in the five-sided figure of Table 4C and would express in percent the amount of similarity between any two species on the basis of the 19 characters of Table 2. The higher values, in this case, mean the higher similarity between species. The percent values for similarity (Table 4A) appear on the right side of the dendrogram (Table 4B) and are indicated on the dendrogram by the broken horizontal bars. The clustering of the first two species, *Meconella oregana* and *M. californica,* is at 85 percent similarity. The next clustering on the dendrogram is at 60 percent and is obtained by averaging the similarity values between *Meconella denticulata* and *M. californica* (55 percent) with that between *Meconella denticulata* and *M. oregana* (65 percent). The clustering of *Platystemon* and *Hesperomecon* is read directly from the table at 55 percent. The value between each combination of *Platystemon* with the three species of *Meconella* (averaging 23.3 percent) and between each combination of *Hesperomecon* with the three species of *Meconella* (averaging 28.3 percent) is reaveraged for the final clustering at 26 (25.8) percent similarity on the dendrogram.

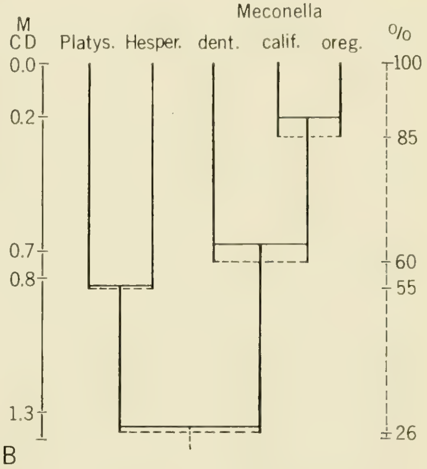
The superposed dendrograms (Table 4B) are similar but, since the methods of analysis were different, the scales of the vertical lines also are different and cannot be compared directly. The information content in either case is relative and the order of the clustering of the species, which is the same in both cases, seems more important than the lengths of the vertical lines. The dendrogram provides an impartial and graphic estimate of similarities among the five species of Platystemonoideae based upon comparative information. It indicates the closeness of the phenetic relationship among the species of *Meconella* and the disparity between these species and both *Platystemon* and *Hesperomecon.* It also shows that *Hesperomecon* (sometimes treated as a species of *Meconella*) has slightly more in common with *Platystemon* than with *Meconella.*

It remains now to offer an interpretation of the dendrogram as a possible phylogeny. My assumptions are that all Platystemonoideae are highly advanced organisms, they ultimately had a common ancestor, the species with most similar morphology likely have diverged from one another most recently, and the least similar have been separated for the longest period of time from a common ancestor. Rates of evolutionary changes probably were not uniform, we have no idea of extinct forms, and we are at a loss to detect mega-mutations of the past which might have given rise to intersecting lines or development leading to cryptic convergences and/or parallelisms. We only can deal with what we have, not with what we wish we had.

TABLE 4. Similarities among the five species of Platystemonoideae.—A, hand tabulation of matching similarities from Table 2: smaller sized numerals in upper right are percent equivalents for larger numerals in lower left. —B, superposed dendrograms: values shown at left and with solid horizontal bars redrawn from computer printout calculated from Table 3 by weighted pair-group method; values shown at right and with broken horizontal bars are hand calculated averages from percentages shown in A. —C, comparison of rounded-off Mean Character Differences among species from Table 3; the lowest value indicates greatest similarity; highest indicates least similarity.

	Platys.	Hesper.	M. dent.	M. calif.	M. oreg.
Platys.		55	20	30	20
Hesper.	11		45	25	15
M. dent.	4	9		55	65
M. calif.	6	5	11		85
M. oreg.	4	3	13	17	

A


M
CD
0.0
0.2
0.7
0.8
1.3
Platys.
Hesper.
Meconella
dent.
calif.
oreg.
%
100
85
60
55
±26
B

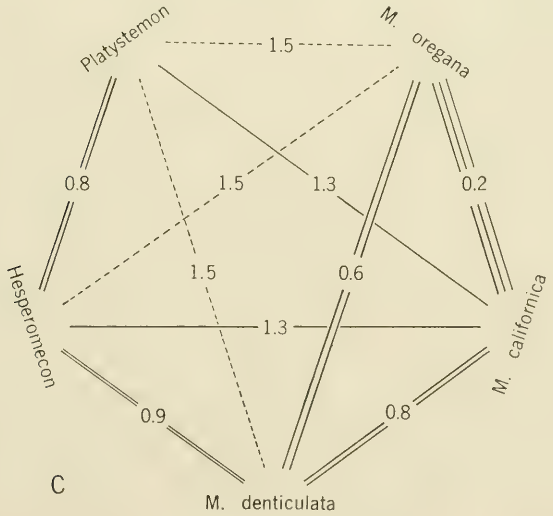

Platystemon
1.5
M. oregana
0.8
1.5
1.3
0.2
Hesperomecon
1.5
0.6
1.3
M. californica
0.9
0.8
C
M. denticulata

Table 4B is a dendrogram of similarities and not a phylogeny but let it serve as one for the purposes of this discussion since it is as good as any that might be proposed. As an hypothetical phylogeny the dendrogram advantageously avoids the symbolism that one modern species is directly descended from another. It suggests that the progenitors of Platystemonoideae probably were somewhat different from present-day taxa and supports my hypothesis that *Platystemon* and *Meconella oregana* probably are phylogenetic dead ends, that neither are prototypes for, nor ancestral to, other living Papaveraceae, and that neither are connecting links to other families. The implications of this conclusion are important in view of the significance previously attributed to the unusual structure of *Platystemon* since I believe that phylogenetic attention should be shifted from *Platystemon* to something perhaps closer to *Hesperomecon*. The reason for this is that the apocarpouslike structure, which has gone unnoticed in *Meconella californica* and *M. oregana,* is just as well developed in these species as it is in *Platystemon.* Within Platystemonoideae, however, the apocarpouslike structure seems more like an innovation than a phylogentic relict. *Hesperomecon* is a convenient model from which both apocarpouslike extremes might have been derived and, at the same time, also serves as an abstract link relating Platystemonoideae to the remainder of the family.

I believe that phylogenetic interpretations based primarily on Besseyanlike dicta (see Thorne 1958, 1963, and many other authors beginning with Bentham 1834) lean too heavily on *Platystemon* as primitive for Papaveraceae and as a connecting link to Ranales without careful examination of *Platystemon* and without attention to the relationship of *Platystemon* to its closest allies. Traditional phylogenetic interpretations of this kind, which suggest that somebody really knows what primitive structure is like, might be correct—but, at the same time, where does one turn for the evidence to support them? In the case at hand, it is not the queer morphology of *Platystemon* but the more conventional morphology of *Hesperomecon* that seems important to me. Apparent sequences in morphological complexity among similar species surely imply relative evolutionary proximity and provide sturdy criteria for taxonomic purposes, but speculations on evolutionary direction or phylogenetic history from morphological data alone are projections into a dimension where too little is known. Furthermore, it is difficult to discuss hypothetical phylogeny and evolutionary similarity without introducing a quagmire of semantic difficulties. The low chromosome number and the nature of the gynoecium (or of other morphological phenomena) do not seem sufficient reason to call *Platystemon* primitive. No fossils are recognized and, regrettably, no inter-taxa hybrids are available for cytological clues to the more recent past of Platystemonoideae.

CONCLUSION

Platystemonoideae is one of four coordinate clusters of taxa within Papaveraceae and whether it has any claim to phylogenetic antiquity relative to other Papaveraceae certainly is not clear. The most generalized element of Platystemonoideae is *Hesperomecon* which seems satisfactory as an evolutionary model for this subfamily, but it does not seem to be a very promising connecting link to other families. It is significant that the phylogenetic position of *Platystemon*, depending on the facts one tends to recognize, can be rationalized either as primitive or advanced, and in the end we know very little more about phylogeny than in the beginning.

THE GENUS **CANBYA** (SUBFAMILY PAPAVEROIDEAE)

For the sake of completeness in this review of *Platystemon* and its allies it seems appropriate to discuss the genus *Canbya* Parry ex A. Gray, at least briefly, since Greene (1903, p. 156) and some other authors have thought it "intimately related" to Platystemonoideae. The genus *Canbya* is typical of subfamily Papaveroideae (Ernst 1962a, b) and the two-fold purpose of including it now is to illustrate the unique features of Platystemonoideae and to eliminate *Canbya* from Platystemonoideae. The species names appear in the following key but are not treated taxonomically.

The genus *Canbya* is composed of two species and is distinguished vegetatively by the diminutive size of the plants, the linear terete and compactly arranged leaves, and the absence of elongated flowering shoots. The plants are glabrous. The flowers are borne on relatively long peduncles and are similar to those of Platystemonoideae with trimerous perianth, twelve or six stamens in a single series, and a gynoecium of three carpels. The genus fundamentally is different from Platystemonoideae, however, in that the stigmatic regions of the three carpels are fused into a single structure with greatly developed, downwardly directed appendages in the commissural position (Fig. 11). The glossy black seeds are dispersed by means of intracarpellary valves in the wall of the fruit which open basipetally along regular lines of dehiscence. The pollen is tricolpate and the chromosome number is $n=8$, but multivalents and extra chromosome material sometimes are present. The cytology of both species needs to be restudied.

The distinguishing characteristics of *Canbya aurea* S. Wats. are the bright golden yellow petals which normally are quickly deciduous, the approximately 12 stamens, and the distribution in the sagebrush plains of southern Oregon and extreme northwestern Nevada (Fig. 1). In contrast, the petals of *C. candida* Parry ex A. Gray are white and somewhat more persistent, there only are about six stamens, and the species is limited to the Joshua Tree woodland of the western Mojave Desert in Southern California (Fig. 1).

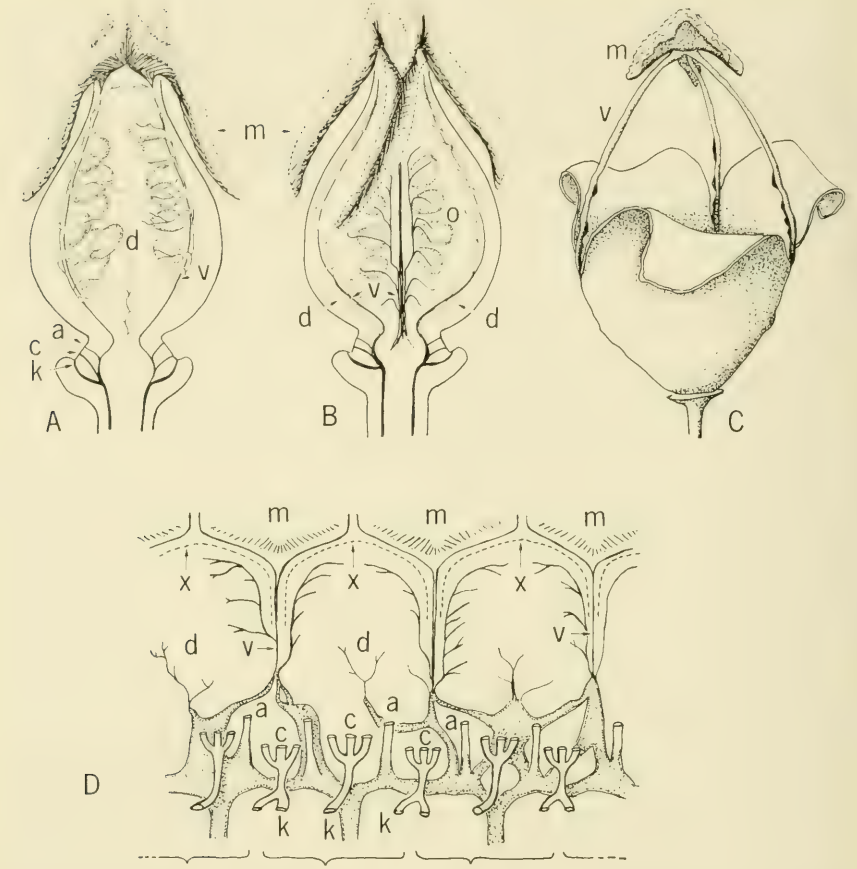


FIG. 11. Diagrams of vascular patterns in flowers and the capsular fruit of *Canbya* (Subfam. Papaveroideae). —A-C, *C. aurea, Ernst 191:* A, ovary drawn as though partially transparent showing duplex commissural appendages of stigmas and longitudinal section of receptacle, X 27; B, same as A turned through 120°; open fruit showing united stigmas, intracarpellary valves reflexed, and persistent placental bundles, X 23. —D, *C. candida, Ernst 138:,* vertical diagram of vascular pattern, diameter of receptacle ca 0.5 mm. —a, stamen traces; c, petal traces; d, dorsal bundles; k, sepal traces; m, duplex commissural appendages of stigmas; o, ovules; v, placental bundles; x, margins of intracarpellary valves; horizontal brackets enclose sepals.

Floral morphology. The peduncles contain six vascular bundles in *Canbya aurea* but only three in *C. candida* (Fig. 11D); in both species the receptacle framework is dissected by irregular gaps. The vascular pattern of the perianth is similar to that of *Platystemon* and *Hesperomecon,* but the sepals of *Canbya,* for their relatively small size, are uncommonly thickly vascularized. The stamen traces in *Canbya* are arranged in a single cycle for both species. The vestigial dorsal bundle of the carpel is represented only by a few short, often branched threads of tracheary tissue. The placental bundle is well developed, consisting of three main branches near the base. The central branch, near the top of the ovary, divides into two portions which continue into the adjacent stigmatic regions to either side. The lower main branches divide repeatedly, sending veins inwardly to the ovules and peripherally to the ovary wall. The basic branching of the placental bundle recalls somewhat that of *Hesperomecon.* Toward the upper part of the ovary in *Canbya,* the main branch of the peripheral system curves toward the median portion of the carpel. As the fruit matures, a line of cleavage separates a valve in the carpel wall from the heavy middle branch of the placental bundle. The fundamental difference between *Canbya* and Platystemonoideae thus is demonstrated by the persistent, fused stigmatic mechanism which is permanently united to the persistent, main portion of the placental bundle, both remaining behind when the valves in the ovary wall open basipetally (Fig. 11C).

When the diagrams of *Meconella, Hesperomecon,* and *Canbya* are compared, there is correspondence between the position of the bundles in the peduncles and the position of the sepals and dorsal traces to the carpels (Figs. 4, 9, 11). The relative arrangement is preserved even though alternate bundles in the peduncles are lost. The bundles that are lost in *Meconella* and in *Canbya candida* are the ones that are alternate with the dorsal traces to the carpels. The apparent reduction series observed in the two species of *Canbya* recalls the reduction series preserved in Platystmonoideae since there is a loss of vascular bundles in the peduncle, reduction in number of stamens, and a reduction to obsolescence of the dorsal trace to the carpel. It is notable that differences in internal structure between the two genera *Hesperomecon* and *Meconella* also exist between the two species of *Canbya.*

Synopsis of Canbya. A discussion of the position of *Canbya* within Papaveraceae only can be meaningful in a full account of subfamily Papaveroideae. It is coincidence, I believe, that *Canbya* and *Meconella* appear to have so much in common. The valvular dehiscence within the carpel wall of the fruit which, at maturity, leaves behind the persistent placental bundles and the fused stigmatic mechanism, clearly isolates *Canbya* from Platystemonoideae. In taking into account the whole of the family, it would seem that *C. candida* may culminate a reduction series within Papaveroideae while *Meconella oregana* culminates a reduction series within Platystemonoideae. This view supports my hypothesis that the similarities between *Canyba* and Platystemonoideae are manifestations of highly advanced form in Papaveraceae and that *Canbya* probably can have played no direct role in the evolution of Platystemonoideae. Whether Platystemonoideae might have played a part in the ancient evolution of *Canbya* is less clear.

KEY TO THE SPECIES

A. Gynoecium of 3 carpels, the stigmas united and with a prominent reflexed lobe over the placentae; fruit wall opening by valves between the persistent placentae; leaves linear, terete; plants glabrous [Subfam. Papaveroideae—*Canbya*].

B. Petals yellow; stamens about 12, the anthers shorter than filaments; mostly southern Oregon. .... [6. *C. aurea.*]

BB. Petals white; stamens about 6, the anthers as long as filaments; Southern California. .... [7. *C. candida.*]

AA. Gynoecium of 3 or more carpels, the stigmas free; fruit wall cleaving through placentae without formation of intracarpellary values (Subfam. Platystemonoideae).

C. Basal leaves broadly linear without petiole; plants pubescent; stamens usually many; fruits not narrowly linear.

D. Gynoecium of more than 3 carpels, each forming a separate locule around a central chamber, the fruit shattering into 1-seeded segments, the fruit wall adhering to the seeds. .... 1. *Platystemon californicus.*

DD. Gynoecium of 3 carpels, the seeds glossy black, free of fruit wall. .... 2. *Hesperomecon linearis.*

CC. Basal leaves distinctly spatulate, narrowed at base; plants glabrous or with only a few hairs on sepals; fruits narrowly linear (*Meconella*).

E. Receptacle about as broad as long, without rim; stamens 6, the anthers frequently as long or longer than filaments. .... 3. *M. denticulata.*

EE. Receptacle broader than long, with small rim beneath insertion of sepals; anthers very much shorter than filaments.

F. Stamens about 12 (sometimes fewer), biseriate or unequal. .... 4. *M. californica.*

FF. Stamens 4-6, in one series, about equal in length. .... 5. *M. oregana.*

SUBFAMILY PLATYSTEMONOIDEAE ERNST,
Jour. Arnold Arb. 43: 317. 1962.

Colonial vernal herbs of the western United States, at first caespitose or rosette forming, often with elongated flowering shoots from the base, sometimes decumbent. Leaves ± alternate below but opposite or whorled above. Flowers terminal on long peduncles. Sepals 3, petals 6, stamens hypogynous, frequently with expanded or toothed filaments. Gynoecium syncarpous but with discrete stigmas; median carpellary traces present reduced or sometimes absent. Carpels 3 or more, disassociating in fruit without the formation of intracarpellary valves, dehiscent through the placentae. Hairs multicellular-multiseriate; pollen 3-colpate; seeds many, small, without arils. Type genus: *Platystemon* Benth.

Platystemon Benth., Trans. Hort. Soc. London II. 1: 405. 1834.

Plants villous, leaves broadly linear, not narrowed at base. Stamens many, carpels more than 3, each forming a separate locule around a central chamber. Ovary ± oblong, the wall constricted between and ± adnate to seeds; carpels disassociating in fruit and shattering into 1-seeded nutlets. Cotyledons linear. Peduncles with 6 vascular bundles. A monotypic genus. Type species: *P. californicus* Benth.—Cream cups. (Fedde recognized 57 species, mostly described by Greene, but the characters seem too indistinct for specific segregation.)

1. **Platystemon californicus** Benth., Trans. Hort. Soc. London II. 1: 405. 1834.

Flowering plants 3-30 (or 60) cm tall, erect to decumbent; leaves 1-9 cm long; peduncles to 25 cm long; flowers to 3.8 cm diam, petals white to cream colored, sometimes with bright yellow marking and/or reddish-purple margins. Fruit to 1 cm broad, to 2.5 cm long; stigmas linear, to 1 cm long; carpels rarely fewer than 5, frequently about 20 (or more), sometimes inserted in more than 1 whorl per flower. Chromosome number $n=6$ (plus occasional supernumeraries).

Type: Dried plants and plants grown from seeds gathered in California by David Douglas are mentioned in the original commentary. The specimen at Kew collected by Douglas and bearing the annotation of Bentham and the stamp of the Bentham Herbarium should be accepted as the lectotype for this species. The locality of the collection in California is unknown. In the original publication, the epithet *californicum* was used.

This species was presented in a paper under the title "Report on some of the more remarkable hardy ornamental plants raised in the Horticultural Society's garden from seeds received from Mr. David Douglas, in the years 1831, 1832, 1833," and was "Read before the Horticultural Society, January 21, 1834." The title page for this volume of the Transactions is dated 1835 but circumstantial evidence in addition to the early presentation date suggests that the paper should be dated 1834. A separately repaged reprint of this paper is dated 1834 (original at Dudley Herbarium, Stanford University) and it clearly is stated by the printer as "From the Horticultural Transactions." The renumbering of the pages suggests that the printer may not have known what the pagination would be for the formal binding of the Transactions. The paper also is reproduced in the French language in Ann. Sci. Nat. II. 2: 80-89, with 1834 as the title page date for the volume and a printer's dateline on page 81, of "Aout," August. All of the included review papers are dated for 1834 or earlier. Whether it was the original printing of Bentham's paper for the Transactions or the repaged reprint that was circulated first is anybody's guess. For convenience, it is easier to cite the reference in the Transactions than the reprint, and the date for both probably is 1834 rather than 1835. Bentham's paper includes the original descriptions for nine new species of Papaveraceae from California, some of them representing new genera.

Distribution: OREGON (Coos Bay, Coos Co.), southward through CALIFORNIA including the islands of S. Miguel, S. Nicolas, Sta. Barbara, Sta. Catalina, Sta. Cruz, Sta. Rosa, and West Anacapa, into northern BAJA CALIFORNIA; and discontinuously in ARIZONA and local in southwestern UTAH (Fig. 1). Primarily below 3000 ft. alt. in California. Slopes, fields, seashore, sand dunes, grasslands, open oak and/or pine woodlands, to desert. Flowering from February until June.

The altitudinal range in California is from near sea level to 100-200 feet both coastally and inland, north as well as south. The occurrence at 7400 ft alt. in the Panamint Mts., Inyo Co. (*Hall & Chandler 6958,* UC), is remarkable. Other highest records in mountains of Southern California are Kern Co., 4200 ft.; Mt. Pinos, 5500 ft.; S. Antonio, 5700 ft.; Cajon Pass, 3800 ft.; near Victorville, 3200 ft.; Deep Springs, 4550 ft.; and S. Jacinto, 4600 ft. These compare favorably with altitudes beyond the California boundaries such as Baja California, to 3450 ft.; Arizona, 1350-4350 ft.; Utah, to 4500 ft. The southernmost locality in Baja California probably is at 30°2′ N. Lat. (*Raven, Mathias, & Turner 12664,* UC). The species also is recorded for Guadalupe Island, Mexico (*Brandegee,* 20 March 1897, UC), which straddles 29° N. Lat. about 160 miles west of Baja California, but it has not been recollected from this island and probably is extinct there now. The populations in grasslands of California may extend over some acres with much variation in form, size, pubescence, and color. Besides the occasional yellow markings on the petals, the most obvious variants are plants with succulent, broad leaves (occasionally maritime); with particularly shaggy pubescence (Ventura and Kern Cos.); with nodding fruits (Baja California, San Diego Co., and insular); or plants nearly glabrate.

Hesperomecon Greene, Pittonia 5: 146. 1903.

Platystigma Benth., Trans. Hort. Soc. London II. 1:406. 1834, not R. Brown, 1832.

Plants villous, leaves broadly linear, not narrowed at base. Stamens many (to few), carpels 3. Ovary with single locule, urceolate to ellipsoidal, the carpels partially disassociating from the top in fruit, the seeds lustrous black and free. Cotyledons linear. Peduncles with 6 vascular bundles. A monotypic genus. Type species: *Platystigma lineare* Benth.=*Hesperomecon linearis* (Benth.) Greene. (Fedde recognized 9 species, mostly described by Greene, but the characters seem too variable for specific segregation.)

The name *Platystigma* of Bentham is rejected for Papaveraceae because Robert Brown used the name earlier for an Old World genus of Euphorbiaceae which now is submerged in the genus *Platea* Bl. of Icacinaceae. In creating *Hesperomecon,* Greene (1903, p. 139) observed that his new genus and *Platystemon* "have often been seen to be so exactly alike in habit, foliage, pubescence, color of flowers and form of stamens, that the best botanists, in order to be able to say which was . . . which . . . would be obliged to examine the pistils; even these, at the first flowering stage [are] not always so very different at first glance, as they are destined to appear when mature."

2. **Hesperomecon linearis** (Benth.) Greene, Pittonia 5:146. 1903.

Platystigma lineare Benth., Trans. Hort. Soc. London II. 1:407. 1834.
Platystemon linearis (Benth.) M. K. Curran, Proc. Calif. Acad. Sci. II. 1:242. 1888.
Meconella linearis (Benth.) A. Nels. & Macbr., Bot. Gaz. 61:31. 1916.
M. linearis var. *pulchella* (Greene) Jeps., Fl. Calif. 1:558. 1922.

Flowering plants 5-30 cm tall; leaves 1-8 cm long; peduncles to 16 cm long; flowers to 3.5 cm diam; petals white to cream colored, sometimes with bright yellow marking and/or suffused with reddish-purple margins. Fruits to 0.6 cm diam and to 1.5 cm long; stigmas to 4 mm long, ± deltoid, revolute margined. Chromosome number, $n=7$.

Type: Described from dried material collected in California by David Douglas, the locality unknown. The specimen at Kew collected by Douglas, bearing the annotation of Bentham, and the stamp of the Bentham Herbarium, should be accepted as the lectotype for this species. (See bibliographical note under *Platystemon californicus* concerning date of publication for original description.)

Distribution: CALIFORNIA. San Francisco, Contra Costa, and Tuolumne counties southward to Los Angeles Co., and discontinuously in Butte Co. (Fig. 2). Primarily below 3000 ft. alt. but as low as 75 ft. (Contra Costa Co.) and to 3300 ft. (Kern Co.); generally lower in northern and coastal regions, higher (above 1000 ft.) in the south. Sand dunes, grasslands, open oak and/or pine woodlands. Flowering from February to June.

The distribution is entirely within that of *Platystemon,* with which *Hesperomecon* often grows, but the range is less extensive and the plants are less common. The localities in the San Joaquin Valley such as near the towns of Minturn, Madera, Tulare, as well as near McKittrick are remarkable. North of San Francisco the species is quite rare with the northernmost record in Butte Co. (*Heller 14537,* UC, US). The following dubious localities are noted: Siskiyou Co. (*Rattan,* DS); Fort Ross (*Wrangell,* US); Tomales (*Andrews,* JEPS). If this species occurs in Marin, Sonoma, or Siskiyou counties it must be exceedingly rare and newer collections with definite locality would be most welcome. I doubt very much that the species occurs in Oregon as given by Peck (1941, ed. 1, p. 320) who may have included it on the basis of Fedde (1909, p. 102) who referred to an ancient specimen at the Gray Herbarium bearing no other information than "Oregon ex D. C. Eaton." In Peck's second edition (1961, p. 350), the notation was changed to *Meconella californica,* which also is an error for Oregon.

The closeness between Bentham's *Platystemon californicus* and his "*Platystigma lineare*" was recognized by Curran (i.e., K. Brandegee) as early as 1888 when she made the combination *Platystemon linearis.* It is ironic that *Hesperomecon linearis,* the type species for the genus, has been submerged in *Meconella* since 1916 even though the more obvious morphological relationship is with *Platystemon.* No one could mistake the plants of *Hesperomecon* for a species of *Meconella;* however, their similarity to plants of *Platystemon* is pronounced and confusing at first glance. Plants of *Hesperomecon* tend to have more compact rosettes, are less likely to have elongated flowering shoots, and the leaves are narrower and frequently seem somewhat more acute but usually are minutely truncated. A positive identification, however, requires an examination of the gynoecium which, in this case, is urn shaped to obpyriform or ellipsoidal, three lobed, and composed of only three carpels, each with distinct, deltoid (seldom linear) stigma with revolute margin.

Sometimes *Platystemon* and *Hesperomecon* are found in close proximity as indicated by the frequent mixture of the two on herbarium sheets, perhaps having been gathered in the same handful of plants. In the La Panza Campground, San Luis Obispo County, *Hesperomecon* and *Platystemon* grow side by side and are very similar except for the ovary. Variation in *Hesperomecon* parallels, more or less, the variation in *Platystemon* although there does not seem to be a form with nodding fruits or an unusually pubescent phase. Smaller plants of *Hesperomecon* occur in Kern County where nearby populations of *Meconella californica* seem unusually similar. In this region *Hesperomecon,* normally with many stamens, may have as few as 10 or 11 arranged, more or less, in two series or sometimes as few as six stamens; however, this similarity is unusual and the shape of the ovary and the basal leaves serve to distinguish these plants from *Meconella,* which in this region also may have a reduced number of stamens relative to the plants of more northern localities. Reduction in number of stamens to about seven also has been noted in San Luis Obispo County. Plants with petals marked with yellow are occasional.

Meconella Nutt. in Torr. & Gray, Fl. N. Am. 1: 64. 1838.

Plants glabrous or with a very few short hairs on sepals, basal leaves spatulate, distinctly narrowed at base, the limb more or less deltoid to orbiculate, the upper leaves more or less linear. Stamens 4-6 in one series or about 12 and biseriate; carpels 3. Ovary linear-oblong with a single locule. Fruit narrowly linear, elongating to 10 or 15 times the length at anthesis, frequently spirally twisted, the carpels disassociating from the top, the seeds lustrous black and free. Cotyledons spatulate. Peduncles with 3 vascular bundles. A genus of 3 species. Type species: *M. oregana* Nutt. in Torr. & Gray. (Fedde recognized 6 species.)

3. **Meconella denticulata** Greene, Bull. Calif. Acad. Sci. 2: 59. 1886.

Platystemon denticulatus (Greene) Greene, Fl. Franciscana 283. 1892.
M. kakoethes Fedde, Rep. nov. spec. 3:275. 1907.
M. oregana var. *denticulata* (Greene) Jeps., Fl. Calif. 1:599. 1922.

Flowering plants 3-21 cm tall, sometimes decumbent; leaves occasionally denticulate, the basal distinctly spatulate, to 3.5 cm long, the blade to 5 mm wide, the petiole to 3 cm long; upper leaves linear to 3.8 cm long; peduncles to 4 cm long; receptacles relatively deep and broad but without rim below sepals; flowers to 1.4 cm diam; petals white, occasionally with small obscure greenish or yellowish spot near base; stamens 6, anthers linear-oblong, frequently half as long or longer than filaments. Fruits to 2.5 mm diam, to 3 cm long; stigmas to 1 mm long. Chromosome number, n=8.

Type: Greene, 27 March 1885, Temecula Canyon, north of San Luis Rey, San Diego Co.; only known specimen at GH.

Distribution: CALIFORNIA. Monterey, Santa Barbara, Ventura, Los Angeles, Orange, Riverside, and San Diego counties, also Santa Cruz Island (Fig. 3). Altitude from about 1000 to 3000 ft. (Los Angeles Co.); between 450-1200 ft. Sta. Cruz Island. Moist slopes in partly shaded opening of chaparral or oak-pine woodlands, frequently with cryptogams. Flowering from March to May.

Not known to me from north of Tassajara Hot Springs, Monterey Co., but dubiously occurring as far north as Castroville (*Brandegee,* April 1889, US). The absence of a receptacle rim, the well vascularized sepals, the often elongated anthers on short filaments, the occasionally denticulate margins of the leaves, and the distribution in coastal Southern California distinguish this species. Toward the southern portion of the range the plants tend to have longer anthers and shorter filaments.

4. **Meconella californica** Torr. & Frém., Report. Expl. Expd. Rocky Mts. 312. 1845.

Platystemon oreganus (Nutt.) M. K. Curran, Proc. Calif. Acad. Sci. II. 1:242. 1888, in part.
Platystemon torreyi Greene, Fl. Franciscana 283. 1892.
Meconella oregana var. *californica* (Torr. & Frém.) Jeps., Fl. Calif. 1:558. 1922.
M. collina Greene, Pittonia 5:143. 1903.
M. octandra Greene, Pittonia 5:142. 1903.

Flowering plants 3.5-18 cm tall; basal leaves 0.5-2.5 cm long, the blade to 5 mm broad, the petiole to 17 mm long; peduncles to 12 cm long; receptacles with small fleshy rim beneath insertion of sepals; flowers to 2.2 cm diam; petals white or cream colored or inner petals white and outer petals yellow; stamens about 12, biseriate, unequal in length, anthers ovoid to orbiculate, much shorter than the filaments. Fruits to 5 cm long and to 1.5 mm in diam; stigmas to 5 mm long, linear. Chromosome number, n=8.

Type: Frémont, probably in 1844, American fork of the Sacramento River; two sheets, the only known specimens, deposited at NY.

The name of the species usually is given as Torr. in Frém. but the original publication attributes the name to Torr. and Frém., although there is every reason to believe that the technical botanical work was exclusively that of Torrey.

Distribution: CALIFORNIA. Sonoma to Santa Cruz counties coastally, and discontinuously from Butte to Kern counties in the western foothills of the Sierra Nevada (Fig. 3). In costal regions occurring from an altitude of about 250-1000 ft. and from about 500 ft. (Butte Co.) to 2800-3000 ft. (Kern Co.) in interior. On sunny moist slopes in oak- douglas fir association coastally or oak and/or pine woodland interiorly and sometimes on or near serpentine soil. Flowering from February to June.

The inclusion of this species in the flora of Oregon by Peck (1961, ed. 2, p. 350) probably is an error as there are no specimens cited for documentation. The species is distinguished by the presence of the small receptacle rim, the single unbranched vein in the sepals, the biseriate and unequal stamens with small anthers, the slow development of the dorsal trace to the carpels, and the paired ventrals in the placentae. The plants in the Coast Ranges seem only to have white petals. Some of the plants of the interior have white petals and others have inner petals white or cream colored and the outer petals yellow, the only example in the family of a truly two-colored corolla. The yellow color, as discussed previously under the heading of Color, is sensitive to daylight, fading at night to white but regenerating in daylight to yellow. The colored phase possibly deserves taxonomic recognition but the plants do not seem very distinctive morphologically, and it does not seem possible to tell whether the type collections was colored or not.

5. **Meconella oregana** Nutt. in Torr. & Gray, Fl. N. Am. 1: 64. 1838.

Platystemon oreganus (Nutt.) M. K. Curran, Proc. Calif. Acad. Sci. II. 1:242. 1888, in part.

Flowering plants 2-10 cm tall; basal leaves to 1.8 cm long, petiole to 1 cm long, blade to 3 mm wide; peduncles to 5 cm long; receptacles with small fleshy rim beneath insertion of sepals; flowers to 11 mm diam; petals white; stamens 4, 5, or 6, the anthers minute, ovoid and much shorter than the filaments. Fruits to 2.5 cm long, to 1.5 mm diam, stigmas to 1 mm long. Chromosome number, n=8.

Type: Nuttall, in 1835 on "open plains of the Oregon [now Columbia River] near its confluence with the Wahlamet [now Willamette River]." This would seem to place the type locality somewhere near Portland, but the only specimens known to me with definite locality for this region are from considerably further east along the Columbia River. Two sheets collected by Nuttall in Oregon are preserved at Kew and three sheets, probably of type material, are deposited at the Gray Herbarium. This is the type species for the genus and the only one known to occur in Oregon.

Distribution: BRITISH COLUMBIA (Vancouver Island), and southward through WASHINGTON, including Orcas, San Juan, and Whidbey islands, and discontinuously southward to Jackson and Josephine counties in OREGON (Fig. 1). Local and rare in CALIFORNIA as noted below. Most plants are presumed to occur below 1000 ft. alt. Sandy bluffs, meadows, and partly sunny moist banks. Flowering from March to June.

The northernmost limit probably is Jesse Island, Departure Bay, Vancouver Island (*W. Spreadborough*, 17 April 1910, GH, CAN) at about 49°12′ N. Lat. The occurrence in California is unexpected but documented. The species has been noted by Rossbach & Rossbach (1940) on the eastern slopes of the Mt. Hamilton Range, Santa Clara Co., and I have collected it in this region in the Arroyo Bayo at an altitude of about 1500 ft. (*Ernst 413, 509,* DS; *J. T. Howell 4662,* CAS; *Rossbach & Beaver 665,* DS). My living plants as well as herbarium specimens were indistinguishable from a culture of plants originating from the high banks of the Columbia River, Oregon, between Mosier and The Dalles at an altitude of about 700 ft. (*Ernst 252,* DS) when compared at Stanford. The airline distance between these two localities is almost 600 miles and it nearly is 300 miles from Mt. Hamilton to the nearest locality in Oregon. Some other collections from the vicinity of the Alameda-Contra Costa county line near Berkelely, California, may be referable to *M. oregana* and are noted (*Chandler 884, Helsley 163, Mason 3666, Tracy 1796,* all UC; *J. W. Blankenship,* 3 Mar. 1892, GH, with 6 very unequal stamens). Some of these plants, however, are confusingly similar to *M. californica* (e.g., *Tracy 1796* has up to 9 stamens and they are unequal) and it is possible that both species are represented in these collections. I have not been able to study living plants in this region.

The species is distinguished by the small receptacle rim, the single unbranched vein in the sepals, relatively narrow petals, and about 4 to 6 stamens whose anthers frequently appear to be inserted somewhat obliquely on the filaments. Frequent irregularities such as fused parts (stamens to petals); fewer parts than expected (missing petals or stamens); or irregularities in the symmetry have been observed. The receptacle rim is sufficient to separate this species from *M. denticulata,* but in the case of incomplete or depauperate specimens, it only is the number and unequalness of the stamens which ultimately distinguishes *M. californica* from *M. oregana.* This accounts for the confusion in the identity of the specimens from the Alameda-Contra Costa region since otherwise the distributional pattern of *M. oregana* and *M. californica* are completely allopatric.

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

A REVIEW OF THE SUBFAMILY CYLINDROTOMINAE IN NORTH AMERICA (DIPTERA: TIPULIDAE)

By

Fenja Brodo

Vol. XLVII Pages 71-115 April 14, 1967 No. 3

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THE UNIVERSITY OF KANSAS
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Vol. XLVII Pages 71-115 April 14, 1967 No. 3

A Review of the Subfamily Cylindrotominae in North America (Diptera: Tipulidae)[1]

By

Fenja Brodo

INTRODUCTION

The Cylindrotominae are the smallest subfamily of the Tipulidae. Members of the group are not commonly collected and are therefore unlikely to appear in general insect collections. Literary references are scattered, with no all-inclusive keys existing to the North American species.

The purpose of this paper is to redescribe the North American species of Cylindrotominae, to construct comprehensive illustrated keys for their identification, to describe and illustrate representative immature stages, and to bring together the pertinent literature about this group.

There is still a difference of opinion concerning the taxonomic rank of this group. Schiner (1864) first recognized these flies as forming a natural taxon, Limnobinae Cylindrotomaeformes, within the tribe Limnobina. Later workers (Brunetti, Needham) retained Cylindrotomini as a tribe of the Limoniinae (Limnobiinae). Others (Kertész, Peus) have considered them as a distinct family. Alexander, Rogers and Takahashi relegate them to a subfamily of the Tipulidae. This latter classification is adopted here.

One North American species of Cylindrotominae was described (from Europe) by Linnaeus (1758), four were described by Osten Sacken in 1865, one by Johnson (1912), and the last to be described were *Phalacrocera occidentalis* and *P. vancouverensis* by Alexander (1927a, b). Immature stages of *Phalacrocera replicata* (from Europe) were first described by De Geer (1773); Cameron (1918) described the larva and pupa of *Cylindrotoma distinctissima americana* (as *C. splendens*), and Alexander (1914b) described the immature stages of *Liogma nodicornis*. The descriptions of the larva and pupa of *Triogma exsculpta* and of the pupa of *Phalacrocera tipulina* are included in this paper. The immatures of *Cylindrotoma tarsalis* and *Phalacrocera occidentalis* are still unknown.

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[1] Contribution No. 1341 from the Department of Entomology, The University of Kansas, Lawrence, Kansas.

After comparing the North American cylindrotomines with those of Europe and Asia (by the examination of some European specimens as well as the literature), I suspect that the genera are ill-defined, as suggested by Alexander (1949), and further study of the subfamily on a world-wide basis may result in the lowering of some of the genera to subgeneric level.

ACKNOWLEDGEMENTS

I wish to express my sincere thanks to Dr. George W. Byers who suggested this study, made much of the material available and advised and encouraged me. To Dr. Charles D. Michener I extend my thanks for his friendly advice and interest. Thanks are due Dr. C. P. Alexander, Amherst, Massachusetts, for his graciousness in loaning me valuable specimens, and to Dr. J. R. Vockeroth, Entomology Research Institute, Canada Department of Agriculture, for descriptions and drawings of the holotype of *P. vancouverensis* and for the loan of many European and American specimens from the Canadian National Collection. I wish also to thank Dr. T. E. Moore, University of Michigan, Dr. P. J. Darlington, Jr., Museum of Comparative Zoology, Harvard University, and Dr. Selwyn Roback, Academy of Natural Sciences of Philadelphia, for the loan of additional specimens.

METHODS AND MATERIALS

Adult specimens either pinned or preserved in alcohol were used for most of this study. Wherever possible, the genitalia of at least one male and one female of each species were boiled for a few minutes in a weak solution of KOH, washed, and placed in glycerine, permitting detailed study with magnifications as high as 54X. The genitalia were eventually placed in microvials pinned under the respective specimens.

All measurements were taken with an ocular grid and are therefore rough, serving only to indicate the general size range of the structures in question. Body length refers to the distance between the vertex of the head (disregarding antennae) to the tip of the abdomen, regardless of the curvature of the body. Wing length is the straight-line measurement from point of attachment to tip.

KEY TO THE SUBFAMILIES OF TIPULIDAE IN NORTH AMERICA (ADULTS)

(modified from Alexander, 1942)

1. Terminal segment of maxillary palpus elongate, whip-like; nasus usually distinct; antennae usually with 13 segments; vein Cu_1 deflected at m-cu, the latter at or close to fork of M_{3+4}; body size usually large. .... *Tipulinae*

Terminal segment of maxillary palpus short; no distinct nasus; antennae usually with either 14 or 16 segments; vein Cu_1 straight, not deflected at m-cu, the latter placed far before fork of M_{3+4}, usually at or close to fork of M; body size usually small or medium. 2

2. Male: aedaegus tripartite (Figs. 1-8), often extruded in dried specimens (Figs. 9-20); female: cerci short, broad (Figs. 21-27); mesonotal suture distinct only in median third of thorax, fading out laterally (Fig. 28); wings not patterned except for pale stigma. .... *Cylindrotominae*

Male: aedaegus having one or two openings; female: cerci elongate, pointed; mesonotal suture distinctly "V-shaped," characteristic of the family; wings often patterned. .... *Limoniinae*

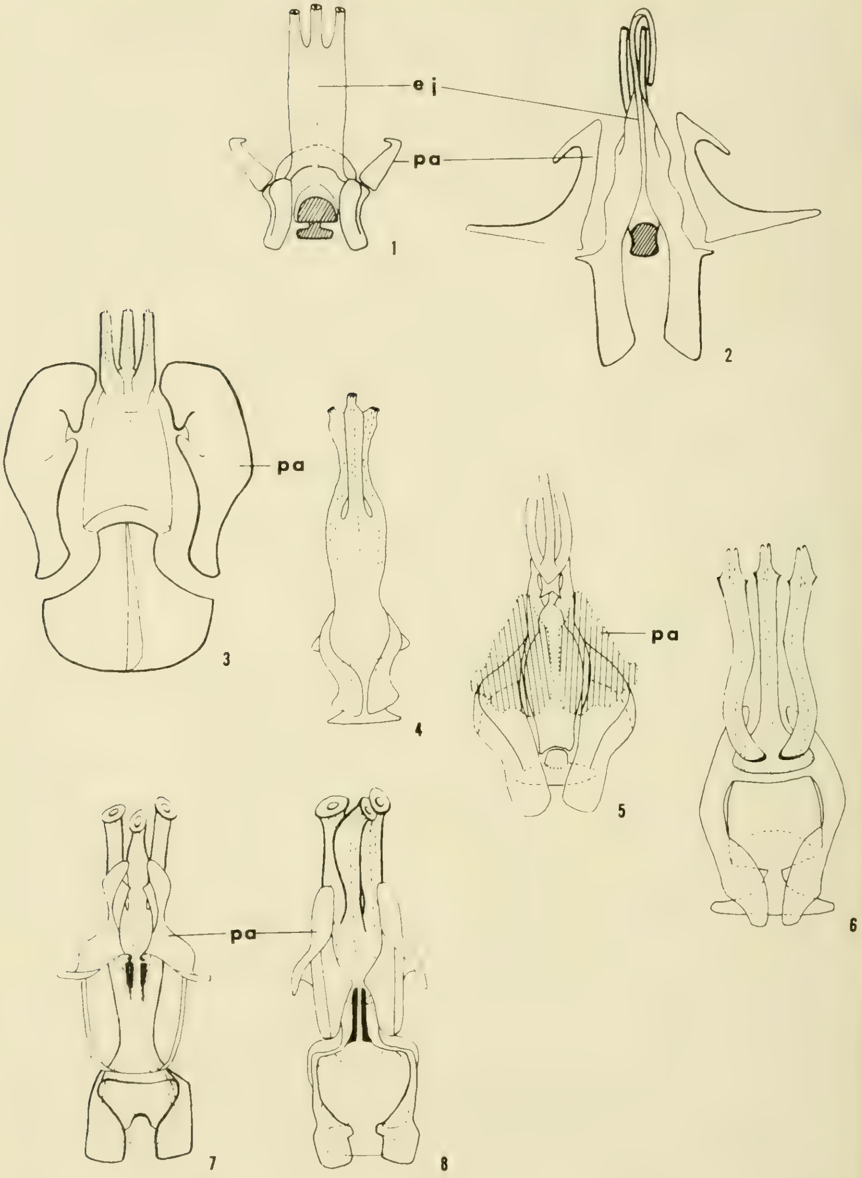
SUBFAMILY **CYLINDROTOMINAE** ALEXANDER

Limnobinae Cylindrotomaeformes Schiner, 1864: 560-563.
Cylindrotomaeformia Osten Sacken, 1865: 234-342.
Cylindrotomina Osten Sacken, 1869: 289-308; 1897: 362-366.
Cylindrotomini Scudder, 1894: 189.
Erucaeformia Bengtsson, 1897: 1-102.
Cylindrotomidae Kertész, 1902: Peus, 1952: 1-77; Takahashi, 1960: 81-91.
Cyttaromini Meunier, 1915: 229-230.
Cylindrotominae Alexander, 1914a: 603-605; 1919c: 926-928; 1920: 959-974; 1927a: 1-16; 1942: 292-296.

This is a curious little subfamily of the Tipulidae comprising 46 species in nine genera. In contrast to the widespread and diverse distribution of the majority of crane flies, the Cylindrotominae are, in general, sparsely scattered over the Holarctic Region, although they also include 14 species in four genera extending southward into the Oriental and Neotropical regions. They usually occur in small, scattered populations in wooded situations at high altitudes, where conditions are typically cool.

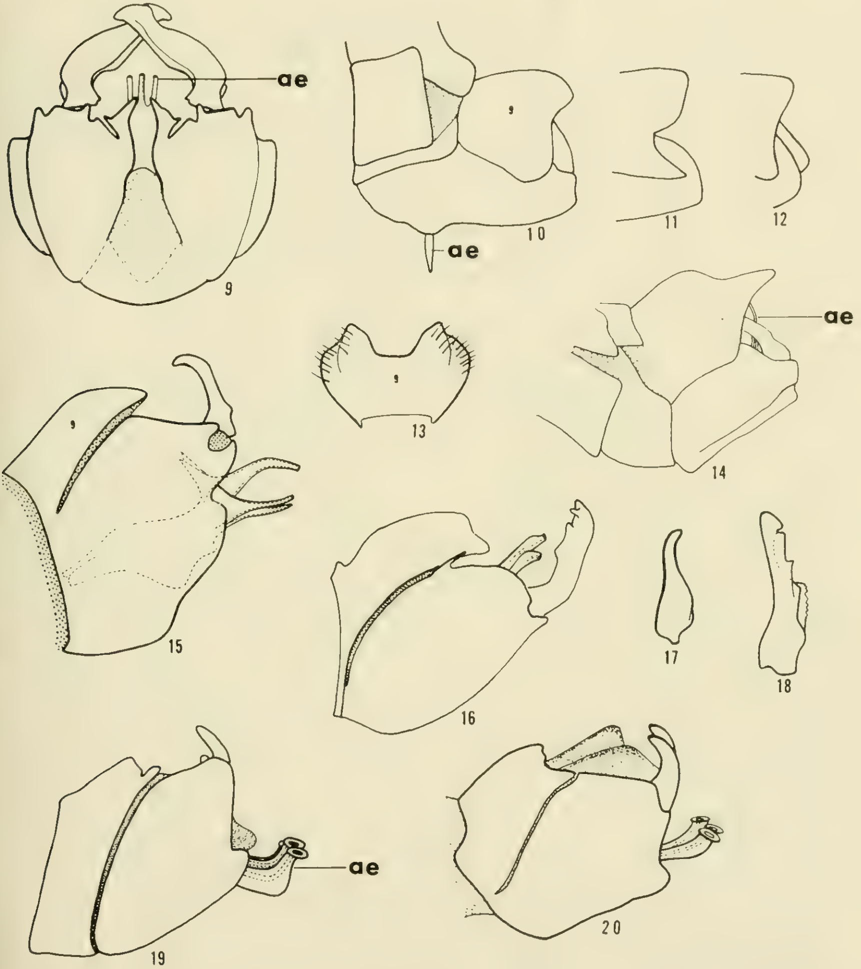
The genera within this subfamily cannot yet be satisfactorily placed in any kind of evolutionary sequence. However, they do fall neatly into two tribes, Cylindrotomini and Stibadocerini, on the basis of the much longer antennae in the latter, as well as several other morphological characters.

The Stibadocerini appear to be the more specialized group morphologically, but their ecology and biology are very inadequately known. The scanty data accompanying specimens indicate that these flies are usually found near small waterfalls and mountain streams at altitudes of 3,000 to 11,000 ft. The combined range of the 14 species of Stibadocerini extends along the southern border of the distribution range of the Cylindrotomini, with nine of these species concentrated in the Oriental Region. All these species (as far as the records indicate) occur at high altitudes where conditions are very similar to those of North America and Europe. Three species are found in the Australian Region (one each in New Guinea, New South Wales and Tasmania), and one isolated species is found in the mountains of Patagonia in southern Chile.



FIGS. 1-8. Aedeagus and accompanying structures, dorsal aspect. ej—ejaculatory duct; pa—paraphyses (gonapophyses, of most authors). Fig. 1. *Cylindrotoma distinctissima americana.* Fig. 2. *Cylindrotoma tarsalis.* Fig. 3. *Phalacrocera occidentalis.* Fig. 4. *Phalacrocera replicata* (=*neoxena*). Fig. 5. *Phalacrocera tipulina.* Fig. 6. *Phalacrocera vancouverensis.* Fig. 7. *Liogma nodicornis.* Fig. 8. *Triogma exsculpta.*

The Cylindrotomini consist of 32 species arranged in five genera (see Peus, 1952; Alexander, 1956b). Only eight of these, representing four genera, occur in North America: *Cylindrotoma tarsalis, C. distinctissima americana, Phalacrocera replicata* (=*neoxena* of other authors), *P. occidentalis, P. tipulina, P. vancouverensis, Liogma nodicornis,* and *Triogma exsculpta.* The



Figs. 9-20. Hypopygia of males. ae—aedeagus; 9—ninth sternum. Fig. 9. *Cylindrotoma distinctissima americana,* ventral aspect. Fig. 10. *Cylindrotoma distinctissima americana,* left lateral aspect. Fig. 11. *Cylindrotoma distinctissima borealis,* left lateral aspect. Fig. 12. *Cylindrotoma distinctissima distinctissima,* left lateral aspect. Fig. 13. *Cylindrotoma distinctissima americana,* ninth tergum. Fig. 14. *Cylindrotoma tarsalis,* left lateral aspect. Fig. 15. *Phalacroera tipulina,* left lateral aspect, showing position and outline of aedeagus. Fig. 16. *Phalacrocera replicata* (=*neoxena*), left lateral aspect. Fig. 17. *Phalacrocera occidentalis,* left dististyle, outer aspect. Fig. 18. *Phalacrocera vancouverensis,* left dististyle, outer aspect. Fig. 19. *Liogma nodicornis,* left lateral aspect. Fig. 20. *Triogma exsculpta,* left lateral aspect.

richest cyclindrotomine fauna is in the Orient (China, Japan and India), where there are nine species of *Cylindrotoma,* three *Phalacrocera,* seven *Liogma,* two *Triogma* and two *Diogma.* The European species are *Cylindrotoma d. distinctissima, C. d. alpestris, C. d. borealis, Phalacrocera replicata, Diogma glabrata* and *Triogma trisulcata.*

GEOLOGICAL RECORD

The earliest information concerning the geological history of the Tipulidae comes from the Mesozoic; however, this is rather inconclusive, and it is not until the lower Tertiary that undisputed tipuline forms occur. In the North American Eocene (such as the White River and Green River beds) and in the Oligocene (the Florissant shales, etc.), there is evidence of an extraordinary development of the Cylindrotominae. In the White River basin they almost dominate the known crane fly fauna, in sharp contrast to their paucity and irregular distribution within the fauna of today.

Many fossil finds have been erroneously placed in this subfamily, but the only fossil genus now generally accepted as belonging to the Cylindrotominae is *Cyttaromyia,* with *Cyttaromyia fenestrata* Scudder (1877) the type species. This genus is extraordinarily similar to the modern genus *Cylindrotoma,* which is also confined to the Holarctic and is distinguished from the former only by having an additional crossvein in cell R_5 forming another closed cell in the wing. *Cylindotoma* specimens having this additional crossvein are occasionally found (Fig. 46). Cockerell (1920) described a new species from the Eocene (White River, Colorado) which appeared to lack this vein, and he therefore placed it with question in the genus *Cylindrotoma* as *C. veterana.*

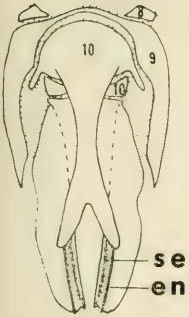
Of the five genera in this holarctic group, it is generally accepted that *Cylindrotoma* is probably the most advanced genus, although a form very similar to this genus is postulated as having given rise to the other four genera (Alexander, 1927a).

Fossil record of North American Cylindrotominae to date:

From the Eocene:
- *Cyttaromyia fenestrata* Scudder, 1877, White River, Utah.
- *C. fuscula* (Cockerell 1920, as *Asilopsis*), White River, Colorado.
- *C. reclusa* Cockerell, 1924, Green River, Colorado.
- ? (*Cylindrotoma*) *veterana* Cockerell, 1920, Roan Mountain, Colorado.

From the Oligocene:
- *Cyttaromyia cancellata* Scudder, 1894, Florissant, Colorado.
- *C. clathrata* Scudder, 1894, Florissant, Colorado.
- *C. oligocena* Scudder, 1894, Florissant, Colorado.
- *C. princetoniana* Scudder, 1894, Florissant, Colorado.

The above species seem to be most closely related to North American species of *Cylindrotoma.*



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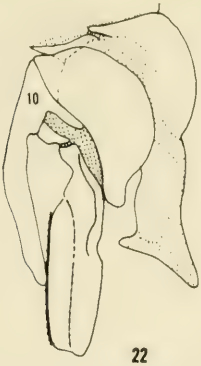

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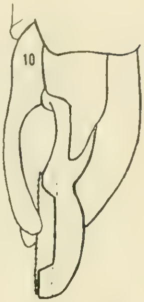

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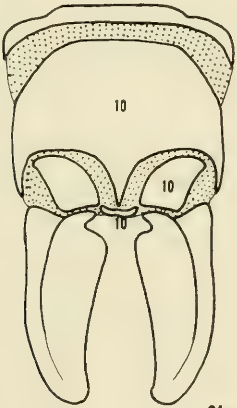

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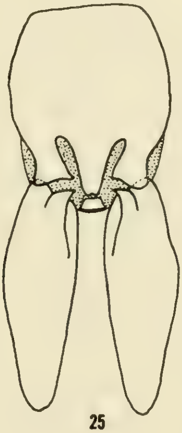

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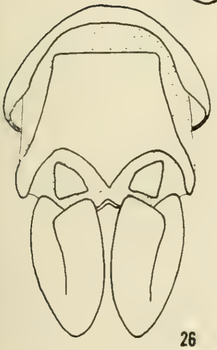

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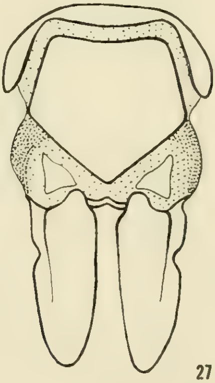

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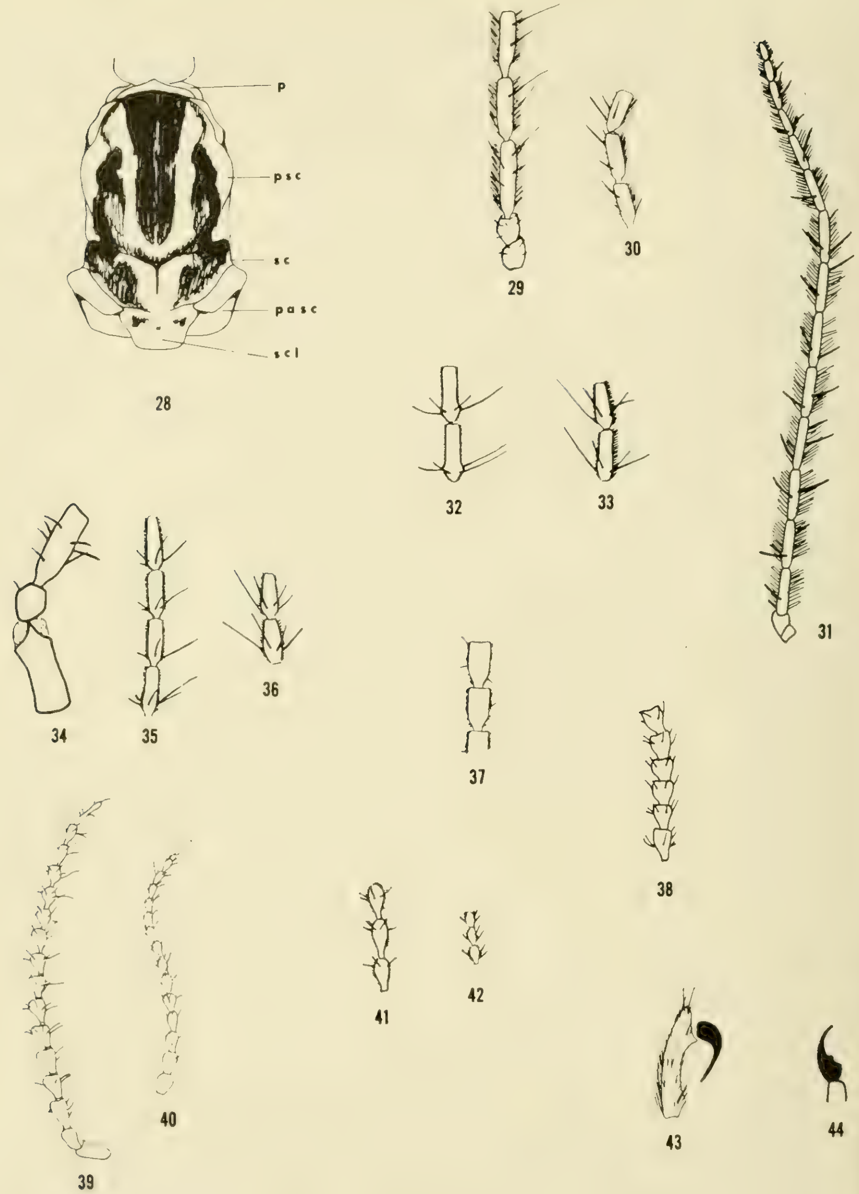
FIGS. 21-27. Female terminalia. 9—ninth tergum; 10—tenth tergum; en—entire edge; se—serrated edge. Fig. 21. *Cylindrotoma distinctissima americana,* dorsal aspect. Fig. 22. *Cylindrotoma distinctissima americana,* right lateral aspect. Fig. 23. *Cylindrotoma tarsalis,* right lateral aspect. Fig. 24. *Phalacrocera tipulina,* dorsal aspect. Fig. 25. *Phalacrocera replicata* (=*neoxema*), dorsal aspect. Fig. 26. *Liogma nodicornis,* dorsal aspect. Fig. 27. *Triogma exsculpta,* dorsal aspect.



FIGS. 28-44. Structural details of Cylindrotominae. p—pronotum; pasc—parascutellum; psc—prescutum; sc—scutum; scl—scutellum. Fig. 28. *Cylindrotoma tarsalis,* thorax, dorsal aspect. Fig. 29. *Cylindrotoma distinctissima americana,* male, scape, pedicel and three flagellar segments. Fig. 30. *Cylindrotoma distinctissima americana,* female, three typical flagellar segments. Fig. 31. *Cylindrotoma tarsalis,* male antenna. Fig. 32. *Phalacrocera occidentalis,* male, 2 typical flagellar segments. Fig. 33. *Phalacrocera occidentalis,* female, 2 typical flagellar segments. Fig. 34. *Phalacrocera tipulina,* male, scape, pedical and first flagellar segment. Fig. 35.

It is curious that no Cylindrotominae have been found in the lower Oligocene Baltic Amber of Europe. According to paleoecologists, the Baltic region in the lower Oligocene was covered with *Pinus succinifera,* an amber-producing pine growing on very mountainous terrain cut by rushing mountain streams. This was a humid and densely shaded environment, judging by the total lack of any specimens requiring arid or sunny conditions and the presence of Trichoptera and other insects which thrive in cool, damp situations. The dipterous fauna in the Baltic amber most closely resembles that which now inhabits eastern North America between 32° and 40° latitude (Alexander, 1931).

TRIBE **CYLINDROTOMINI**

Diagnosis: The Cylindrotomini (which include all North American species of the subfamily Cylindrotominae) are characterized by medium body size (8-16 mm) and legs which are considerably shorter than those of Limoniinae of equivalent body size. The wings are slightly suffused with brown and sometimes have in addition a pale oval stigma but never possess any other kind of pattern. The antennae are 16-segmented. The thorax has at least a faint indication of 3 broad longitudinal stripes, giving a characteristic pattern to this group of flies. The mesonotal suture is curved instead of "V-shaped" and does not extend beyond the median prescutal stripe. The male hypopygium is broad and bears only 1 pair of dististyles. The aedeagus divides into 3 tubes distally and is often found protruding in dried specimens. The female terminalia are short and broad in contrast to the much longer and more slender external genital apparatus found in most species of the other 2 subfamilies. The blade-like cerci are dorsal to and partly overlap the hypovalves.

Description: Antennae 16-segmented, longer in male than in female; scape with small, toothlike lateral projection (Fig. 34); palpi 5-segmented, last segment sometimes lengthened, often almost as long as first 4 combined but never exceeding these segments in length; clypeus short, with apical tuft of hairs but no "nasus"; first cervical sclerite very tiny or apparently absent; second cervical sclerite large, quadrate.

Pronotum typically divided into 3 areas by two longitudinal furrows, anteriorly a ridge, medially a more or less raised crest, posteriorly a ridge split and flattened medially. Pretergite glabrous, generally paler than rest of thorax; mesonotum with 3 more or less distinct broad longitudinal stripes,

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Phalacrocera tipulina, male, 4 typical flagellar segments. Fig. 36. *Phalacrocera tipulina,* female, 2 typical flagellar segments. Fig. 37. *Phalacrocera replicata* (=*neoxena*), male, 2 typical flagellar segments. Fig. 38. *Phalacrocera vancouverensis,* male, 6 typical flagellar segments. Fig. 39. *Liogma nodicornis,* male antenna. Fig. 40. *Liogma nodicornis,* female antenna. Fig. 41. *Triogma exsculpta,* male, 3 typical flagellar segments. Fig. 42. *Triogma exsculpta,* female, 3 typical flagellar segments. Fig. 43. *Phalacrocera tipulina,* male, tarsal segment and tarsal claw. Fig. 44. *Phalacrocera vancouverensis,* male, tarsal claw.

median stripe extending from pronotum to mesonotal suture, lateral stripes commencing slightly below median stripe, swelling outwards on scutum, narrowing, almost merging behind mesonotal suture; mesonotal suture curved behind median stripe, fading out laterally (Fig. 28) (in *Cylindrotoma* apparently continuing forward along sides of median stripe); anterior edges of scutum raised, more or less giving impression of continuation of mesonotal suture across thorax.

Wings pale brown due to microscopic brown hairs; veins darker brown, costa and distal branches of radius and media bearing brown macrotrichia, other veins bare; pale, oval stigma usually present. Subcosta ending unbranched before stigma or joining costa or radius, or dividing, Sc_1 ending in costal cell, Sc_2 turning posteriorly (Fig. 49, Sc_{2A}) to join R_1 for a short length, then anteriorly (Sc_{2B}) to join costa; branches of Sc often fragmented. Radius with 2 or 3 branches reaching costa; tip of R_{1+2} usually obliterated, R_2 considered to have fused with R_1 just beyond area of stigma, often present only as a very short, almost obliterated crossvein (Fig. 53); R_3 and R_{4+5} reaching costa independently. Three or 4 branches of media reaching costa: M_1 and M_2 not separated in *Liogma* and *Triogma;* M_3 and M_4 not separated in *Phalacrocera replicata, P. tipulina* and *P. vancouverensis.* Cubitus straight, not bent at junction of m-cu, but sharply curved distally, joining wing margin perpendicularly. Two anal veins, as characteristic of the family.

Abdomen long, broad posteriorly, more slender and darker anteriorly. Ninth tergum variously lobed or notched. Basistyles large, broad, indistinctly separated medially by membranous region; single pair of dististyles, simple or armed with small projections. Aedeagus[2] tripartite distally (bipartite in the European *Diogma*) enclosing 3 ejaculatory ducts (lateral ducts in *Cylindrotoma* apparently vestigial). Variously shaped scleritized plates closely associated with basal end of aedeagus (lacking in *Phalacrocera occidentalis* and *Cylindrotoma tarsalis,* but probably represented by basal developments of aedeagus in the latter). Paraphyses (Figs. 1, 2, 3, 5, 7, 8) 2 variable sclerites on either side of or above aedeagus.

FEMALE terminalia: Ovipositor short, broad; cerci broad, flat, entire or with serrated dorsal edge; hypovalves lightly sclerotized, fused to eighth sternum or separated by thin membranous region. Tenth tergum fragmented: large flat sclerite with median and often with two lateral projections caudally (in *Cylindrotoma* median projection much prolonged and forked distally),

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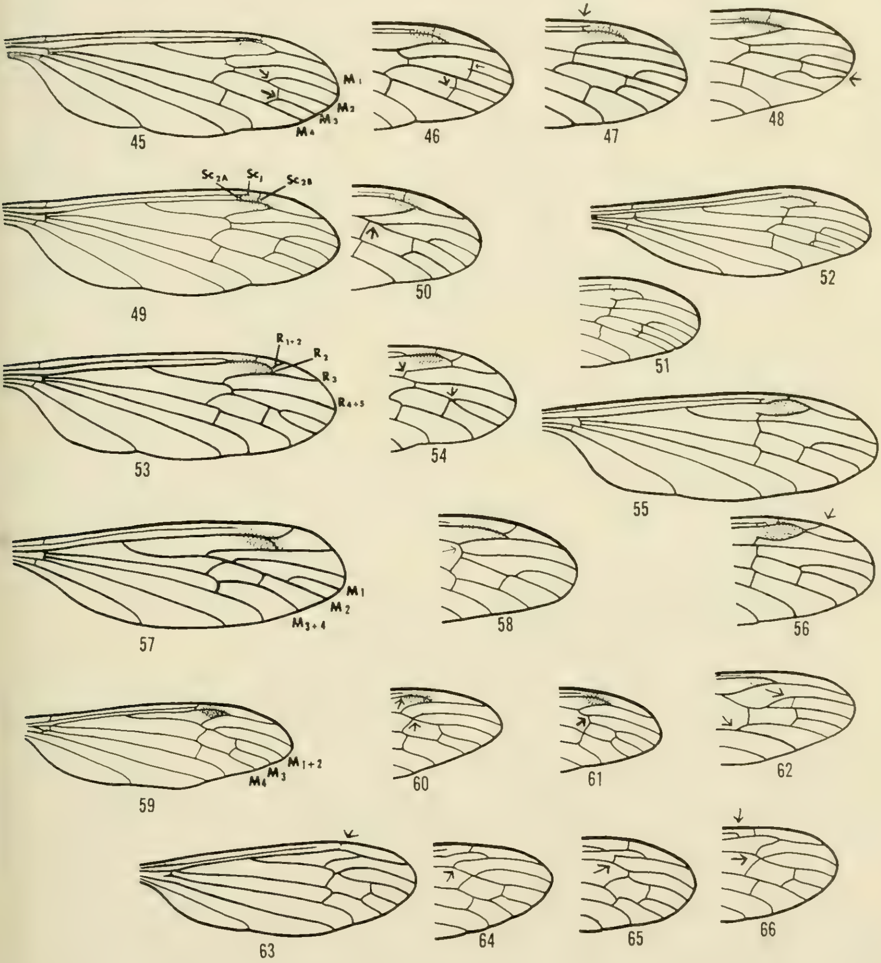
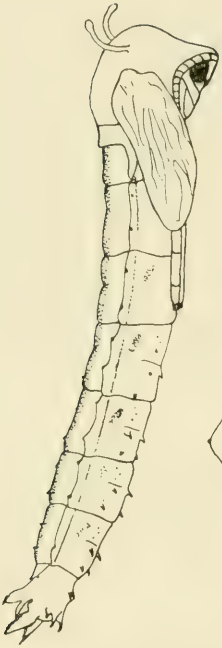
[2] The morphology of the aedeagus and its accompanying structures is confusing. Snodgrass (1904), studying the hypopygium of *Phalacrocera tipulina,* concluded that the penis (aedeagus) might actually represent a fusion of the penis and its guard (adminiculum). The aedeagus of *P. tipulina* has a bifurcate, dorsal, scleritized prolongation, reminiscent of the adminicular rods of *Dolichopeza* (see Byers, 1961).

2 small sclerites on either side (attached in *Phalacrocera replicata* and *Triogma trisulcata* of Europe), and narrow sclerite between bases of cerci. Three sclerotized spermathecae visible in cleared specimens.

One suspects that the cylindrotomine genera are ill-defined when noting the striking similarity between *Triogma* and *Liogma,* both of which genera include only one North American and one European species. The insecure taxonomic position of *Phalacrocera occidentalis,* which has been shifted between *Phalacrocera* and *Cylindrotoma,* testifies to the inadequate definition of



FIGS. 45-66. Wings of Cylindrotominae. M—media; R—radius; Sc—subcosta; arrows—call attention to variations in venation. Figs. 45-48. *Cylindrotoma distinctissima americana.* Figs. 49-50. *Cylindrotoma tarsalis.* Figs. 51-52. *Phalacrocera occidentalis.* Figs. 53-54. *Phalacrocera replicata* (=*neoxena*). Figs. 55-56. *Phalacrocera tipulina.* Figs. 57-58. *Phalacrocera vancouverensis* (58=holotype). Figs. 59-62. *Liogma nodicornis.* Figs. 63-66. *Triogma exsculpta.*



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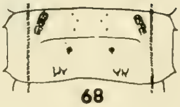

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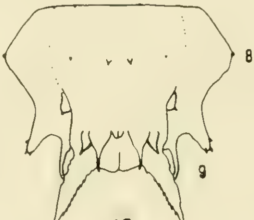

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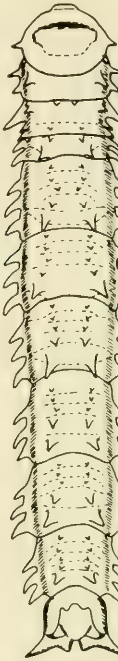

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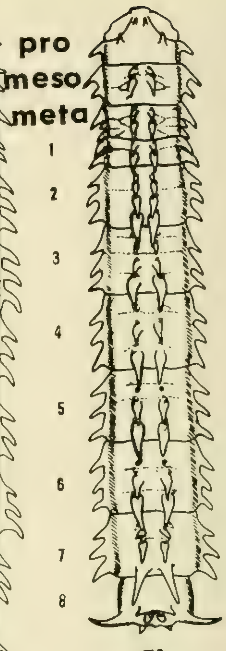
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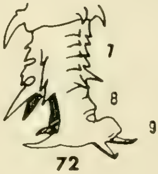

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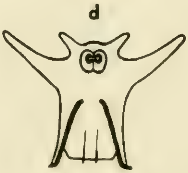

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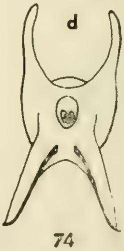

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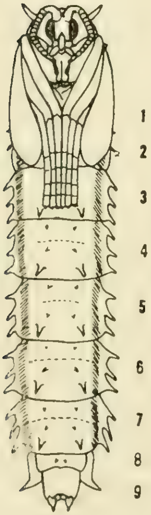

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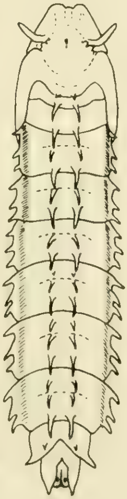

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FIGS. 67-76. Figures showing immature stages. d—dorsal aspect; 1, 2, 3 etc.—refer to abdominal segments. Fig. 67. *Phalacrocera tipulina*, pupa, right lateral aspect. Fig. 68. *Phalacrocera tipulina*, pupa, ventral aspect of typical abdominal segment. Fig. 69. *Phalacrocera* these two genera. A world-wide study of this group with particular emphasis on the more diverse Asian species should lead to a better delineation of the genera.

KEY TO THE GENERA OF **CYLINDROTOMINAE** OF NORTH AMERICA (adults)

1. Stout, dark flies, distinctly rugose or punctate on head and thorax. .... *Triogma*

   Slender bodied flies without such punctations. 2

2. Thoracic dorsum with whitish or yellowish-grey pubescence; pleurae pubescent, dull black or brown. .... *Phalacrocera*

   At least part of thorax pale yellow, 3 more or less distinct black stripes on prescutum, thorax dull or shiny but not pubescent. 3

3. Shiny mahogany-brown or black stripes on prescutum; 3 branches of media reaching wing margin (Fig. 59); cerci smooth, rounded blades (Fig. 26); antennae nodulose, almost cordate in male (Fig. 39). .... *Liogma*

   Dull brown or black stripes on thorax; 4 branches of media reaching wing margin (Fig. 45); cerci with serrated edges dorsally (Figs. 21, 22, 23); antennal segments cylindrical (Figs. 29, 30). .... *Cylindrotoma*

The following keys to the larvae and to the pupae are provisional since the immatures of several species remain unknown. The diagnosis of *Phalacrocera* is based on the characteristics of *P. replicata, P. tipulina* and *P. vancouverensis.* The immature stages of *P. occidentalis* are not known. The diagnosis of *Cylindrotoma* is based solely on *C. distinctissima* subspecies since the immatures of *C. tarsalis* are not known.

KEY TO THE LARVAE OF **CYLINDROTOMINAE** OF NORTH AMERICA

(modified from Alexander, 1927a)

1. Body appendages very long, filiform and dichotomously branched dorsally. .... *Phalacrocera*

   Body appendages short. 2

2. Dorsal appendages simple, in a single median row on abdominal segments 3-7; terrestrial on spermatophytic plants. .... *Cylindrotoma*

   Dorsal appendages in pairs with teeth or with small protuberances anteriorly. 3

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tipulina, pupa, ventral aspect of posterior segments. Fig. 70. *Triogma exsculpta,* larva, ventral aspect. Thoracic segments indicated as pro, meso, meta. Fig. 71. *Triogma exsculpta,* larva, dorsal aspect. Fig. 72. *Triogma exsculpta,* larva, right lateral aspect of posterior segments. Fig. 73. *Triogma exsculpta,* spiracular disk of larva. Fig. 74. *Liogma nodicornis,* spiracular disk of larva (redrawn from Alexander, 1920). Fig. 75. *Triogma exsculpta,* female pupa, ventral aspect. Fig. 76. *Triogma exsculpta,* female pupa, dorsal aspect.

3. Two pairs of processes on spiracular disks (Fig. 74); dark, oblique, lateral marks on abdominal terga. .... *Liogma*

   Three pairs of processes on spiracular disks (Fig. 73); abdominal segments brown dorsally, whitish at edges. .... *Triogma*

KEY TO THE PUPAE OF **CYLINDROTOMINAE** OF NORTH AMERICA

(modified from Alexander, 1927a)

1. Abdominal terga 3 to 7 without processes or lobes. 2

   Abdominal terga 3 to 7 with lobes on each segment. 3

2. Abdominal sterna bearing small spines; mesonotal[3] respiratory horns elongate, directed backwards (Figs. 67, 68). .... *Phalacrocera*

   Abdominal segments unarmed; mesonotal respiratory horns small, directed slightly forward. .... *Cylindrotoma*

3. Two of 3 pairs of lobes on each abdominal tergum (Fig. 76). .... *Triogma*

   A single pair of long slender lobes on each abdominal tergum. .... *Liogma*

Cylindrotoma Macquart

Cylindrotoma Macquart, 1834: 107; Walker, 1856: 268-337; Schiner, 1863: 217-226; Osten Sacken, 1865: 234-237; Alexander, 1920: 927; 1942: 294; Peus, 1952: 67.
Type: Limnobia distinctissima Meigen.

Diagnosis: Cylindrotomini with 3 dull, dark brown or black stripes on pale yellowish prescutum. Four branches of media reaching wing margin. Female cerci distinctly serrate dorsally, partially covered by distal branches of median prolongation of tenth tergum.

Description: Head smooth, bare, very light to dark brown; scape short, round; flagellar segments cylindrical; no hairs anteriorly on pronotum; pretergites pale yellow; mesonotum hairless, pale yellow, often dusky anteriorly, with 3 dark longitudinal stripes on prescutum; mesonotal suture apparently "U-shaped", flanking median stripe, slightly raised edges of scutum giving only faint indication of continuation of mesonotal suture across thorax; scutum partially divided by longitudinal suture; scutellar sutures clearly defined; pleural sclerites pale yellow, black areas on anepisternum, postepisternum, and pleurotergite; mesepisternum with transverse suture; longitudinal suture on pleurotergite; wings faintly suffused with brown, oval stigma slightly darker; Sc_1 fading just before stigma, Sc_2 weakly indicated or absent; radius with two branches (R_3 and R_{4+5}) reaching costa; r-m usually present (occasionally lacking in one or both wings); 4 branches of media present, M_1 branching at distal edge of discal cell, M_3 together with short medial cross-

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[3] Byers (1961: 769) noted that the breathing horns of the Tipulidae are mesothoracic not prothoracic as propounded in the literature. I have verified this for the Cylindrotominae.

vein forming distal edge of cell; tibial spurs small, indistinct, close together, covered with appressed microscopic hairs; tarsal claws small, slender. Abdomen varying from dark to light brown, lighter median longitudinal band on dorsum and venter; distal edge of each segment pale.

MALE terminalia: Eighth tergum narrow, entire or partially divided dorsally by narrow membranous area; ninth tergum large, squarish, rectangularly notched medially, produced into 2 lateral lobes distally; aedeagus with three tubes, only middle tube showing complete ejaculatory duct leading to semen pump.

FEMALE terminalia: Eighth tergum not continuous, reduced to 2 narrow lateral sclerites; ninth tergum produced into 2 large lateral areas narrowly joined anteriorly and dorsally; tenth tergum elongate, divaricate distally, with 2 small lateral projections near base, 2 triangular fragments in membrane between tenth tergum and cerci; cerci broad, dorsal margins serrate.

KEY TO ADULTS OF NORTH AMERICAN SPECIES OF CYLINDROTOMA

1. Male with flattened, gently curved aedeagus, aedeagal tubes short, of equal length (Figs. 1, 9); 2 dorsal edges on each female cercus, outer edge entire, inner edge serrate (Figs. 21, 22); tarsal segments brown, slightly darker distally. .... *distinctissima americana*

Males with broadly curved aedeagus, aedeagal tubes elongated, middle tube consideraly longer than lateral tubes (Figs. 2, 14); 2 dorsal edges on female cercus as in *C. distinctissima americana,* but the outer nonserrated edge vestigial, represented only by anterior and posterior vestiges joined basally (Fig. 23); second and third tarsal segments abruptly paler than distal segments. .... *tarsalis*

Cylindrotoma distinctissima americana Osten Sacken

(Figs. 1, 9, 10, 13, 21, 22, 29, 30, 40-48, 77)

Limnobia distinctissima Meigan, 1818: 131.[4]
Cylindrotoma distinctissima; Macquart, 1834: 107.
Cylindrotoma brevicornis Zetterstedt, 1838: 846.
Cylindrotoma americana Osten Sacken, 1865: 236-237; Alexander, 1942: 294.
Cylindrotoma splendens Doane, 1900: 197, pl. 8, fig. 21 (wing); Cameron, 1918: 67-89; Alexander, 1920: 708-710, 967-969, pl. 84 (larva and pupa); 1927, pl. 1, fig. C (wing), fig. 8 (female genitalia), fig. 9 (male genitalia). (New synonymy.)
Cylindrotoma juncta Coquillett, 1900: 401.
Cylindrotoma pallescens Alexander, 1930: 280.
Cylindrotoma splendens pallescens Alexander, 1954: 42. (New synonymy.)
Cylindrotoma distinctissima americana; Alexander, 1956a: 177.

There is much confusion concerning the taxonomic extent of this species. Osten Sacken (1865) characterized *americana* from eastern North America by its three black thoracic stripes, the central stripe being longitudinally divided by a thin yellow line (Fig. 28). He concluded with the observation: "The European *C. distinctissima* seems to be very like *americana* in its color-ing." In 1900, Doane described a western species, *C. splendens,* having black thoracic stripes; no mention was made of a median yellow dividing line on the prescutum, but he noticed three distinct dark spots on the pleurae and minor variations in the radial and medial fields of the wing. My study of *splendens* and *americana* revealed that the thin yellow stripe along the midline of the thorax occurs occasionally in both groups of flies and that both exhibit the same pleural markings.

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[4] Only the basic references to the European *C. d. distinctissima* have been cited.

In 1930 Alexander described *pallescens,* which he differentiated from *splendens* by its much paler and rufous appearance. Later, in 1954, he came to the conclusion that *pallescens* was merely a subspecies of *splendens.* I was able to compare several hundred specimens ranging in the west from Unalaska, Alaska, southward to Colorado and in the east from Nova Scotia southward to New York and westward to Michigan (see Fig. 77). It soon became apparent that coloration is of little use taxonomically, as the same sort of variation exists throughout, and the same held true for slight differences observed occasionally in wing venation. The details of the genitalia are virtually identical throughout. Despite the geographic division of these specimens into eastern and western populations, I consider them to represent one species. There is insufficient evidence or justification for the retention of subspecies within this group.

In a relatively recent paper, Alexander (1956) gave his opinion that *americana* is merely a subspecies of the European *distinctissima.* I am indebted to the Canadian National Collection for the loan of 11 specimens of *distinctissima* from Sweden and the opportunity to compare these in the minutest detail with representative specimens of *americana* from all parts of its range. In almost every structural detail, including those of the genitalia in both sexes, no differences could be found. The Swedish specimens, however, lacked the very pale and rufous form characteristic of some of the American populations, but this may simply be a function of the smaller sample size in the former. Peus (1952) distinguished three subspecies of the European *distinctissima,* and with the help of his drawings and descriptions I was able to differentiate the *americana* group by the shape of the posterior edge of the ninth tergum in the male (Figs. 10-12). Unfortunately this character is of limited use as the exact shape of the tergum is often difficult to determine, due to distortion in drying of the insects.

Diagnosis: Males of this species have a flattened, slightly curved aedeagus, divided distally into 3 short tubes of equal length. Females have a pair of cutting edges dorsally on each cercus, the outer edge smooth, the inner edge serrate. All tarsal segments are brown, but the fourth and fifth are slightly darker.

Description: MALE: Body length 10-12 mm; wing length 8-10 mm. Head pale yellow, dark spot behind antennae, almost square in dorsal profile, slight indentation behind eyes; no pubescence on head, several light hairs posteriorly; palpi, labium, and labrum medium to dark brown, membranous areas lighter; clypeus medium brown, irregularly fringed with hairs, narrow laterally (slightly broader than in *tarsalis*), defined by deep, horizontal fronto-clypeal suture; antennal bases raised anteriorly, close together, narrow furrow between them widening and fading out behind scapes; scape short, brown, lighter apically, slightly longer medially but lacking distinct toothlike projection; pedicel slightly broader than scape; flagellum dark brown with cylindrical segments densely covered with erect hairs as long as width of segments proper; 2 to 4 longer darker hairs on each segment, those more dorsal slightly longer (Fig. 29); eyes not protruding but accented by slight indentation behind; ommatidia small (smaller than in *tarsalis*), black; first cervical sclerite small, narrow; second cervical large, squarish, dark brown.

Pronotum pale yellow to brown, anterior edge slightly curved, broader and higher medially creating depression behind; 2 more or less fused basal spots on postscutellum; halteres dark on knobs, stems lighter, fringed with hairs; coxae pale, inner distal edge black; femora, tibiae brown; tarsi brown, apical segments slightly darker. M_{1+2} branching near distal edge of discal cell.

Terminalia of male: Ninth tergum broad, slightly produced laterally into broad conical lobes (Fig. 13); dististyles heavily sclerotized, haired, broad, with denser tufts of hairs basally, narrower ridged shaft widening anteriorly into round concave head (Fig. 9); aedaegus a flattened, slightly curved blade, divided distally into 3 short tubes of equal length, basally supported by a ventral sclerite and a sclerite on each side (Fig. 1); paraphyses small, slender sclerites lying transversely in membrane between aedeagus and basistyles.

FEMALE: As for male, except for following characteristics: thoracic stripes never attaining dark brown-black characteristic of many males; flagellar segments (Fig. 30) shorter than in male, covered with shorter hairs, several longer hairs dorsally. Terminalia (Figs. 21, 22): Cerci broad flat blades bearing two dorsal cutting edges, separated by narrow sclerotized trough, outer edge smooth, inner edge serrate; ventral edges of cerci sinuous; tenth sternum 2 lightly sclerotized plates with hairs, lying in membrane ventral to cerci; hypovalves membranous and narrowly cleft at tips; 3 identical, spherical, heavily sclerotized spermathecae.

Variation: Variation in amount and distribution of pigments has been the sole basis for differentiating the western group *pallescens* from *splendens* and from *americana* as noted above. Among the specimens which I have studied, three from Nova Scotia (Baddeck, 6 July 1928, D. M. Bates) in addition to 19 from Colorado (Kenosha Pass, 20 June-10 July, 1919) were mottled light orange on the thorax, with the longitudinal stripes barely distinguishable from the background, thus fitting the description of *pallescens*.

The eastern specimens, with the exception of the paler ones from Nova Scotia, had distinct dark stripes (but females never attained the full black of some of the males), and the western specimens from Washington and Oregon varied from almost white to very black. Occasionally fully pigmented specimens of both the eastern and western populations show the yellow dividing line down the middle of the thorax. A series from Klamath Falls, Oregon, 23 June 1959 (G. W. Byers), was intermediate in coloration, containing mostly pale brown specimens and several darker males. Strikingly similar variation in pigmentation has been studied in other insects (Ross, 1956), and experiments have shown that varying humidity and temperature caused the production of different amounts of carotinoids and melanins. Apparently this is a basic physiological reaction, the effects of which are masked in many insects by other pigments or by structural colors.

The wings also exhibit much variation (Figs. 45-48). Traces of Sc_2 are variable, M_{1+2} may divide before or beyond the distal edge of the discal cell, and parts of the media or radius may be weak or almost obliterated. Short spurs are often present, particularly on branches of the media, and one specimen was found with an extra crossvein in cell R_5, creating another closed cell, as in the fossil genus *Cyttaromyia*.

Larva: Living specimens are light chlorophyll green with 2 narrow, pale brown longitudinal lines on dorsum, extending from the posterior end, above spiracles anteriorly, becoming more expanded and diffuse on the fore part of the body. Preserved specimens are brown to light yellow, the longitudinal lines remaining visible. Dorsal processes are simple, in a single median row on abdominal segments three to seven.

Pupa: The live pupa is green. Preserved specimens are pale yellowish. The small mesonotal breathing horns are directed slightly forwards.

Detailed descriptions of larvae and pupae were given by Cameron (1918), Alexander (1920) and Peus (1952).

Ecology: The life history of this species is well-known, having been described in detail by Cameron (1918) and summarized by Alexander (1920). The females have a unique ovipositor equipped with two sawlike blades, enabling them to make incisions in the upper epidermis of leaves of small land plants upon which their larvae will later feed. In the western range of this species, the larvae have been found in rich woodlands, feeding on *Allium, Anemone, Trautvetteria, Stellaria,* and *Viola.* The larvae cease feeding after one molt, hibernate among fallen dead leaves, and finish feeding and molting in the following spring. Females emerge in large numbers before males are seen. Dr. George W. Byers observed near Anchorage, Alaska, on 28 June and 3 July, that this species was locally very abundant in cow parsnip (*Heracleum*) thickets in deep shade and that the adults rest on the upper surface of the leaves or hang from the edge with wings outspread. They were also taken in Klamath County, Oregon, in a swale where *Smilacina sessilifolia* was a common plant.

Cylindrotoma distinctissima americana occurs in northern regions at relatively high elevations. In Colorado, the southernmost tip of its known range, it has been collected at 10,000 ft.; in Oregon and Washington at 3,000-4,000 ft.; up to 7,000 ft. in Montana and British Columbia; 5,000 ft. in New Hampshire; and almost at sea level in Unalaska, Alaska, and Nova Scotia.

Flight records: 6 May-31 Aug.

Distribution (Fig. 77): ALASKA: Admiralty Island, 23 June-26 Aug.; Cascade (15 mi. SE of Anchorage), 28 June -3 July; Cold Bay (163° W 55° N, on tundra), 26-27 July; Igiak Bay, 17 July; Kenai Peninsula (22 mi. N of Seward), 1 July; Unalaska, 24 Aug.; Virgin Bay, (Prince William Sound), 26 June. ALBERTA: 39 mi. SSE of Valley View, 10 July; Waterton Lakes National Park, 23-24 June. BRITISH COLUMBIA: Vancouver District, Squamish Diamond Head Trail (3200-4000 ft.), 5-19 Aug.; Caribou District, Lillooet, Mt. McLean (7200 ft.), 12 June; Kootenay District, Mt. Revelstoke, 26-30 Aug.; Nanaimo District, Vancouver Is.: Forbidden Plateau, Victoria, Westholme, 10 May-18 Aug. COLORADO: Grand Co., Ute

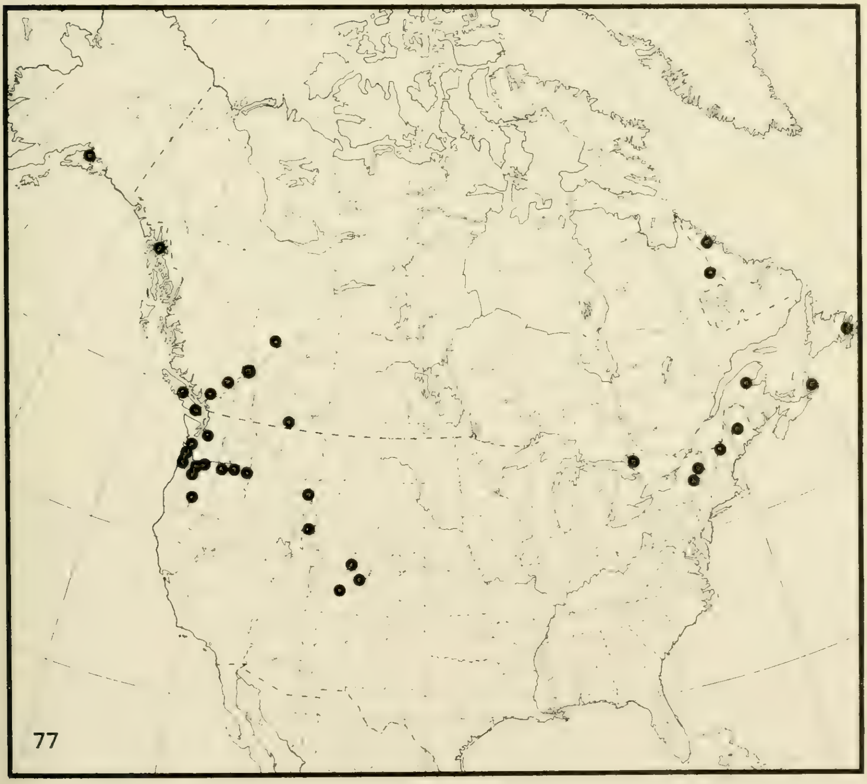

Fig. 77. Range of *Cylindrotoma distinctissima americana.* Each spot represents one or more collections within a county or at a locality.

Pass (Williams Fork Range, 10,500 ft.), 16 July; Gunnison Co., Gothic (9500-10,000 ft.), 16 July; Park Co., Kenosha Pass (10,000 ft.), 20 June-10 July. LABRADOR: Nutak, 26 July. MAINE: Piscataquis Co., Capens, 11 July. NEW BRUNSWICK: (no further data). NEWFOUNDLAND: Bonavista North and South Districts, Terra Nova National Park, 8 July. NEW HAMPSHIRE: Coos Co., Bretton Woods, Glen House, Mount Washington, Lake of the Clouds (5000 ft.), Tuckerman's Ravine (5400 ft.), White Mts., 28 June-31 Aug. NEW YORK: Essex Co., Mt. Marcy, 21-28 July; Fulton Co., Gloversville, 17 June. NOVA SCOTIA: Victoria Co., Baddeck, 6 July. ONTARIO: Parry Sound Co., Burks Falls, Sand Lake, 5-14 Aug. OREGON: Clackamas Co., Still Creek, 16 July; Clatsop Co., Saddle Mt. (Boyer Station), 6 May-18 June; Hood River Co., Cascades (Mt. Hood, Hood River Meadows, 4800 ft.), 17 July-8 Aug.; Klamath Co., SE edge of Crater Lake National Park (4350 ft.), Crater Lake (6200 ft.), Odell Lake (4760 ft.), 23 June-2 Aug.; Linn Co., Big Meadows, North Santiam, 3 Aug.; Morrow Co., Castle Rock, Sourgrass Creek, 13-17 May; Umatilla Co., Blue Mt., Spring Creek (3900 ft.), Little Antone Creek (4100 ft.), Little Phillips Creek (3800 ft.), 5 June-3 July; Wallowa Co., Wallowa Creek (4635 ft.), above Lazy T Ranch (5500 ft.), Lostine Valley Guard Station (4900 ft.), 29 June-17 July; Yamhill Co., High Heaven, 4 May. PENNSYLVANIA: (no further data). QUEBEC: Bonaventure Co., Escuminac, 2-31 July; Indian House Lake (56° 08′ N Lat., 64° 44′ W Long.), 18 July. WASHINGTON: Pierce Co., Cayuse Pass (Mt. Rainier, 4650 ft.), Nisqually Glacier Trail (4000 ft.), Wonderland Trail (above White River, 4900-5000 ft.), 23 July-1 Aug.; Pacific Co., Ilwaco, 5 May. WYOMING: Lincoln Co., Jenny Lake (6780 ft.), Leigh Lake (6870 ft.), 3-12 July; Yellowstone National Park (Northeast Entrance 7200 ft.), Obsidian Creek (7300 ft.), 24-27 June.

Types: C. americana Osten Sacken, two male syntypes (one with broken abdomen), White Mountains, New Hampshire, end of June, 1836 (no. 10237, Museum of Comparative Zoology, Harvard University).

C. splendens Doane, three male syntypes, Unalaska, Alaska, 24 Aug. 1897 (Kincaid) (no. 7,051, U.S. National Museum).

C. juncta Coquillet, female holotype, Virgin Bay, Prince William Sound, Alaska, 26 June (no. 5,204, U.S. National Museum).

C. pallescens Alexander, female holotype, Ute Pass, Williams Fork Range, Grand Co., Colorado, 10,500 ft., 16 July 1929 (C. F. Clagg), (C. P. Alexander Collection, Amherst, Massachusetts).

Cylindrotoma tarsalis Johnson

(Figs. 2, 14, 23, 28, 31, 49, 50, 78)

Cylindrotoma tarsalis Johnson, 1912: 2, fig. 4 (wing); Alexander, 1919c: 963, plate 30, fig. 7 (wing); 1927a: plate I, fig. 1 (wing); 1942: 294, fig. 8 (antenna), fig. G (wing).
Cylindrotoma ? anomala Johnson, 1912: 2-3, fig. 3 (wing).

Diagnosis: In the male the aedeagus is strongly curved, and its median tube is greatly prolonged. The female has a serrated dorsal edge on each cercus, lateral to which lie anterior and posterior vestiges of a smooth edge. The second and third tarsal segments are abruptly lighter than the other leg segments.

Description: MALE: Body length 8-9 mm; wing length 7-9 mm. Head dark brown dorsally, lighter ventrally and laterally, grayish pollinose with fine light hairs posteriorly, broadly oval in dorsal profile, no indentation behind eyes; palpi, labium, labrum medium brown, membranous areas lighter; clypeus light brown, irregularly fringed with hairs, delineated by arched frontoclypeal suture; clypeus narrow laterally (narrower than in *C. d. americana*); antennal bases raised slightly and somewhat further apart than in *americana,* separated by narrow dark brown sclerotized strip; scape and pedicel of equal length, pale yellow or brown; broad tooth on scape; flagellum (Fig. 31) brown, cylindrical segments densely covered with erect hairs the length of diameter of segments, 2 to 4 longer hairs dorsally on flagellar segments, none ventrally; head oval in dorsal aspect, with eyes forming rounded ends ommatidia larger than in *americana,* appearing grayish white within black network; first cervical sclerite small, narrow; second large, approximately square.

Pronotum hairless, pale to dark brown, anterior edge slightly curved, broader and higher medially, creating depression behind; pale brown spot on postscutellum; halteres dark on knobs, stems lighter and fringed with hairs; coxae pale, inner distal edge black; femora, tibiae brown; first, fourth, fifth tarsal segments brown, second and third abruptly lighter. M_{1+2} branching close to distal edge of discal cell.

Terminalia of male: Ninth tergum with 2 narrow lobes (Fig. 14); dististyles sclerotized, simple structures narrowing and curving distally, fewer hairs than in *americana;* median tube of aedeagus much prolonged, curved dorsally; baso-lateral portions of aedeagus much produced on either side; paraphyses large sclerotized "C-shaped" structures on either side of aedeagus (Fig. 2).

FEMALE: Only 2 females seen. Similar to male except for usual sexual dimorphism. Head slightly indented behind eyes; flagellar segments shorter than in male, first 2 segments broadly joined, others showing small basal "neck" region; segments clothed with short hairs, less dense than in male, appressed rather than erect; several longer, darker hairs on dorsal surface of segments. Terminalia (Fig. 23): Cerci broad, flat; serrate dorsal edge on each cercus lateral to which lie anterior and posterior vestiges of smooth blade joined basally, entire central portion of blade apparently never developed; ventral edges of cerci straight; hypovalves membranous at tips, cleft somewhat more deeply than in *americana;* (tenth sternum and spermathecae not observed due to insufficient material).

Variation: The same differences in the amount and quality of pigmentation exist here (at least in the males) as in *C. d. americana.* Occasionally the crossvein r-m is obliterated.

Immature stages: Not seen.

Ecology: These flies apparently frequent the same sort of habitats as *C. d. americana.* They are found at high altitudes, in Hudsonian and high Canadian zones, in small, widely scattered populations, flying from May to September. The adults can be swept from rank vegetation shaded by trees in close proximity to water. The females have serrated edges on their cerci;

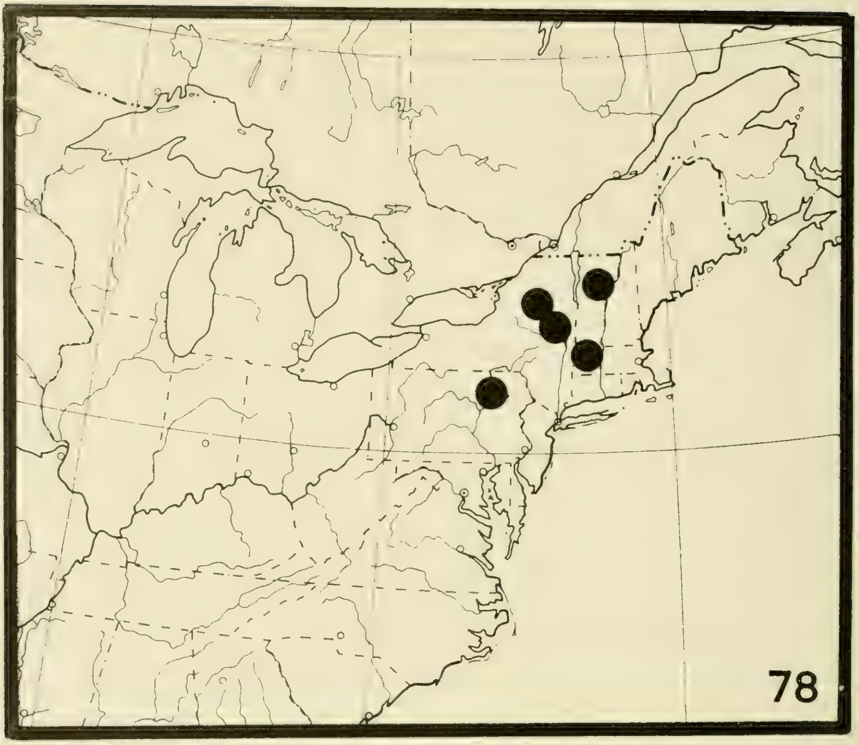

Fig. 78. Range of *Cylindrotoma tarsalis.* Each spot represents one or more collections within a county or at a locality.

thus in this species the eggs are probably laid in incisions of the epidermis of food plant leaves in much the same manner as by *C. d. americana.*

Flight records: 30 May-12 Sept.

Distribution (Fig. 78): CONNECTICUT: Litchfield Co., Norfolk, 12 June-12 Sept. NEW BRUNSWICK: (no further data). NEW YORK: Fulton Co., Bleecker (Woodsworth's Lake, 1650 ft.), Gloversville, 9 June-19 Aug.; Herkimer Co., Indian Castle, 13 June. PENNSYLVANIA: Lycoming Co., 30 May. VERMONT: Lamoille Co., Stowe, 15-24 June.

Types: Male holotype, 6 male paratypes, Woodsworth's Lake, Bleecker, New York, 19 Aug. 1909, (no. 7480, Museum of Comparative Zoology, Harvard University); 7 male paratypes, same data (C. P. Alexander collection, Amherst, Massachusetts).

C. ? anomala Johnson. Female holotype, Woodsworth's Lake, Bleecker, New York, 1 Aug. 1909, (no. 7481, Museum of Comparative Zoology, Harvard University).

Phalacrocera Schiner

Phalacrocera Schiner, 1863: 224; Alexander, 1927a: 9-10; 1942: 292-293; Peus, 1952: 64.
Type: Tipula replicata Linnaeus, 1758 (=*Limnobia nudicornis* Schummel, 1829).

Schiner established this genus on the basis of the presence of R_{1+2} and the sparsely haired flagellar segments. However, neither of these characters is useful, even when only the Palearctic species are considered. The four North American species, *Phalacrocera occidentalis, tipulina, replicata* (=*neoxena*) and *vancouverensis,* form a reasonably homogeneous group, but characters employed in this paper are probably of limited use on a world-wide basis.

Diagnosis: This genus may be recognized by the light pubescence on a black or dark brown head and thorax, almost obscuring the 3 mesonotal stripes, which are only faintly outlined by a thicker pubescence. Either 3 or 4 branches of the media reach the wing margin. The tenth tergum in the female is not greatly elongated and extends only to the base of the cerci. The cerci do not have a serrated dorsal edge.

Description: Head smooth, black or dark brown, covered with whitish or yellowish pubescence; scape longest antennal segment; flagellar segments cylindrical or subcylindrical, sparsely haired or densely covered with extremely short erect hairs; prontum haired; pretergites pale yellow to brown; mesonotum black, pubescent, pubescence thickest along longitudinal lines delimiting thoracic stripes; pleural sclerites black or dark brown; scutellar suture usually indistinct; transverse suture on mesepisterium; longitudinal suture on pleurotergite; wings faintly suffused with brown, oval stigma barely darker; Sc_1 and Sc_2 usually present; radius with 2 or 3 branches reaching wing margin; r-m present; 3 or 4 branches of media reaching wing margin; if only 3, M_{3+4} not branching but continuing directly to wing margin; if 4, pattern as for *Cylindrotoma.* Tibial spurs large, strongly curved and divergent, haired, tips bare; tarsal claws larger than those of *Cylindrotoma.*

MALE terminalia: Eighth tergum entire, narrow; ninth tergum large, squarish, notching at distal edge variable; lateral lobes variable; aedeagus with 3 slender tubes each sheathing an ejaculatory duct.

FEMALE terminalia: Eighth tergum narrow, may be reduced to 2 lateral sclerites; ninth tergum narrow, not produced laterally, tenth tergum variable but never prolonged and forked over cerci; cerci broad, flat, with no distinct serrated edge but occasionally several microscopic, irregularly formed teeth distally.

KEY TO ADULTS OF NORTH AMERICAN SPECIES OF **PHALACROCERA**

1. Pronotum with distinct transverse crest in center; R_{1+2} present. 2

Pronotum almost flat except for shallow horizontal furrow; tip of R_{1+2} usually atrophied. 3

2. Flagellar segments covered with dense coat of short erect hairs, with a few longer irregularly placed hairs (Fig. 32); mesonotal suture broad, shiny brown. .... *replicata*

Flagellar segments with verticils, not covered with short dense hairs (Fig. 38); mesonotal suture narrow, dull and darker than rest of thorax. .... *vancouverensis*

3. Three branches of media present (Fig. 55); median aedeagal tube strongly arched dorsally, lateral tubes parallel and close together (Fig. 15); pronotum glabrous. .... *tipulina*

Four branches of media present (Fig. 51); 3 aedeagal tubes short, straight and parallel (Fig. 3); pronotum pollinose. .... *occidentalis*

Phalacrocera occidentalis Alexander

(Figs. 3, 17, 32, 33, 51, 52, 79)

Phalacrocera occidentalis Alexander, 1927a: 10.
Cylindrotoma occidentalis Alexander, 1954: 41-42.

This species is of particular interest because it resembles both *Phalacrocera* and *Cylindrotoma.* Alexander (1954) placed *occidentalis* in *Cylindrotoma* because it has four branches of the media, although he later (Alexander, 1965) listed this species in *Phalacrocera.* I am recognizing *Phalacrocera occidentalis* because this species seems to resemble the genus *Phalacrocera* more closely in the following respects: The thorax is blackish with a grayish-yellow pubescence. (*Cylindrotoma* species have three distinct black prescutal stripes on a pale thorax.) The mesonotal suture does not flank the median stripe. The longest antennal segment is the scape, and the whorl of hairs on the basal enlargement of the flagellar segments most closely resembles that of *P. tipulina.* The pronotum is flat like that of *P. tipulina,* lacking the median crest of *Cylindrotoma.* The cerci of the female are simple rounded blades, lacking the serrated edge found in *Cylindrotoma,* and the ninth tergum is not prolonged nor divaricate distally. Lastly, the tibial spurs are long and slender, characteristic of *Phalacrocera.* Except for characters of the male genitalia, this species most closely resembles *P. tipulina.*

Diagnosis: This species is black with grayish-yellow pubescence on the head and thorax. The pronotum is broad, flat and pollinose. Four branches of the media reach the wing margin. The semen pump and its apodemes and paraphyses are extremely large in comparison to the three very small tubes of the aedeagus.

Description: MALE: Body length 12 mm; wing length 8-10 mm. Head dorsally black with whitish pubescence, ventrally dark brown glabrous; dorsal profile subtriangular, no indentation behind eyes, eyes confluent with head contour; palpi, labial segments dusky brown, haired, membranous region lighter brown; labrum shiny brown; clypeus dusky brown, pubescent, broad and flat, bearded distally, lateral portions long, at least two-thirds length of anterior region; frontoclypeal suture deep, horizontal; antennae about 5 mm, dusky brown, bases not raised anteriorly; scape longest, broadest segment, lateral teeth narrow; pedicel globular; flagellar segments subcylindrical, covered with extremely short, erect hairs, whorl of longer hairs on enlargement near base of each segment (Fig. 32); first cervical sclerite not seen (insufficient material), second large, black, convex.

Pronotum almost flat, dark brown with yellowish pubescence, short erect hairs anteriorly, shallow furrow bisecting it horizontally; pretergite pale yellow to brown. Mesonotum black with yellowish pubescence; 3 stripes indicated vaguely by denser pubescence in longitudinal furrows flanking region of stripes; narrow line of lighter pubescence longitudinally bisecting mesonotum; mesonotal suture small, almost straight, glabrous brown, scutum black, pubescent, pubescence whiter at scutal suture; scutellum very pale, pubescent, with 2 shiny brown pits anterolaterally; postscutellum with 2 black basal areas, whitish pubescence medially; pleurites light brown to black, pubescent, membranes dusky; pleurotergal suture and suture between anepisternum and preepisternum lacking.

Coxae dark brown, pubescent; trochanters lighter, edged with black distally; femora, tibiae, tarsal segments brown, darker distally; tibial spurs long, diverging, clothed with short brown appressed hairs, darker and bare distally; last tarsal segment cylindrical, claws long, slender and broadly curved, only slightly widened at base. Knobs of halteres dusky black, stems lighter, edged with hairs.

Wings (Figs. 51, 52) pale brown, stigma slightly darker, oval; Sc_1 fading out just before stigma, Sc_{2A} and Sc_{2B} absent or merely suggested by presence of pale lines in wing; 2 branches of radius (R_3 and R_{4+5}) reaching wing margin, (a very small portion of R_{1+2} found on 1 specimen); r-m in line with radial crossvein, joining media near proximal corner of discal cell; 4 branches of media reaching wing margin; M_{1+2} branching at or just beyond distal edge of discal cell, M_{3+4} branching at posterior distal edge of discal cell; short medial crossvein plus section of M_3 form distal edge of discal cell.

Abdomen dark brown to black, posterior segments bordered anteriorly by a colorless band. Terminalia of male (Figs. 3, 17): Ninth tergum with rounded notch medially on distal edge; basistyles without lateral projections; dististyles simple narrow structures, slightly widened at base, yellowish, blackened distally, covered with short fine hairs; aedeagus with 3 short, parallel tubes, large, broad semen pump, but no basal sclerites; paraphyses large, "mitten-shaped" (Fig. 3).

FEMALE: Differs from male in the following characters: antennae shorter (2.5 mm), flagellar segments shorter (Fig. 33), cylindrical, without basal enlargements, clothed with erect hairs slightly longer than in male, whorl of longer hairs basally. Terminalia: (Character of ninth tergum not observed on the one dried specimen); tenth tergum a large sclerite with 3 distal projections, two small triangular sclerites in membrane between projections;

cerci short, broad, haired structures, rounded distally; hypovalves weakly sclerotized, incompletely fused to ninth sternum, narrowly notched and membranous distally.

This description is based on only two specimens, a male and a female, borrowed from Dr. C. P. Alexander, Amherst, Massachusetts.

Immature stages: Not seen.

Ecology: This species has been found in highest, humid Transition or low Canadian life zones in Washington State at 2,800 ft., and at 4,475 ft. in Oregon. Individuals were found in high alpine meadows overgrown with grasses and sedges in the vicinity of a stream. The characteristic plants in this region were clumps of scrubby willow, *Veratrum viride, Habenaria, Caltha leptosepala, Pedicularis groenlandica surrecta, Dodecatheon* and alpine fir, mountain hemlock and pines along streams (see Alexander, 1949).

Flight records: 10 June-8 Aug.

Distribution (Fig. 79): OREGON: Hood River Co., Cascades, (Hood River Meadows, Mt. Hood, 4475 ft.), 17 July-8 Aug. WASHINGTON: Pierce Co., Longmire Springs (Mt. Rainier, 2800 ft.), 10 June, 17 July.

Type: Male holotype, Longmire Springs, Mt. Rainer, Washington, 10 June 1917 (H. G. Dyar), (C. P. Alexander collection, Amherst Massachusetts).

Phalacrocera replicata (Linnaeus)

(Figs. 4, 16, 25, 37, 53, 79)

Tipula replicata Linnaeus, 1758: 587.[5]

Limnobia nudicornis Schummel, 1829: 122.

Tipula brevirostris Zetterstedt, 1838: 844.

Phalacrocera replicata; Schiner, 1863: 224; Grünberg, 1910: 33-35, fig. 33 (antenna), fig. 34 (male terminalia), fig. 35 (female terminalia), fig. 36 (wing); Peus, 1952: 1-77, fig. 2 (head), fig. 4 (thorax), fig. 10 (wings), fig. 17 (tarsal claws), fig. 18 (female terminalia), fig. 23, 29 (male terminalia), fig. 33, 36, 37a, 39, 40, 41, 42, 43, 47, 50 (larvae), fig. 52, 56a, 57a (pupae), fig. 61 (eggs).

Phalacrocera neoxena Alexander 1914a: 603-604, pl. 25, fig. 10 (wing); 1919: 30, fig. 9 (wing); 1927a: pl. 2, fig. 6 (wing); 1942: 293, 295, fig. 33, E (wing).

A comparison of American specimens of *neoxena* with five Swedish specimens of *replicata* indicates that only one species is involved. Alexander (1914a) noted a similarity between these two groups but also pointed out several differences such as color, variations in the radial-medial crossvein and differences in the male genitalia. However, my material afforded detailed comparisons, including comparable preparations of the genitalia of both sexes, and I found approximately the same range of variation in both populations, albeit my European sample was considerably smaller and limited in geographic range.

Diagnosis: This is one of the more robust species in the subfamily. It is black with grayish pubescence on the head and whitish yellow pubescence

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[5] Only the basic European references to this species are given.

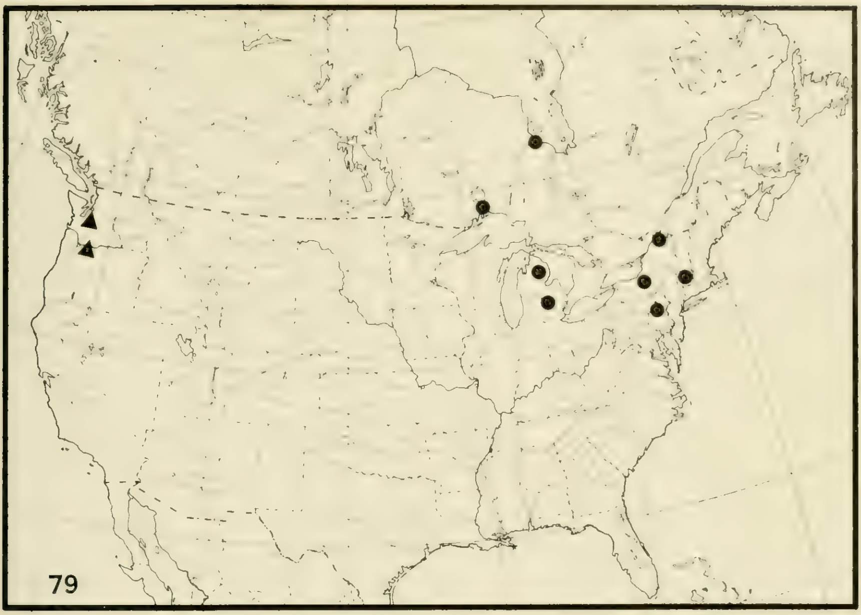

FIG. 79. Ranges of *Phalacrocera occidentalis* (triangles) and *Phalacrocera replicata* (circles). Each spot represents one or more collections within a county or at a locality.

on the thorax. The pronotum is pollinose with dark crest in the center, accented by a furrow behind and flanked by 2 dark spots on either side. Three branches of the media and 3 of the radius reach the wing margin. The 3 aedeagal tubes are long and slender in comparison to the semen pump and its apodemes. The flagellar segments have several long, scattered hairs in addition to a dense covering of very short hairs. The mesonotal suture is broad and shiny brown.

Description: MALE: Body length 12-15 mm; wing length 10-11 mm. Head black, grayish pubescence particularly evident laterally and bordering eyes, several light hairs posteriorly; dorsal profile broadly rectangular with short, narrow "neck", slight indentation behind eyes; labium, labrum, and palpi medium brown, clypeus brown, broadest and most densely haired distally, slight horizontal distal groove giving impression of broad rim; lateral expansion of clypeus somewhat less than two-thirds its length; frontoclypeal suture strongly arched, obscured by coloration; antennae (Fig. 37) about 4.0 mm, dark brown, bases not raised but separated by dark narrow groove; scape subcylindrical, slightly widened apically, about length of first few flagellar segments, lateral teeth broadly triangular; pedicel globular; flagellar segments subcylindrical, each gently tapered proximally, truncate apically, covered with very short, dense, erect hairs with several sparse, irregularly placed longer hairs; first cervical sclerite brown, small, squarish; second cervical sclerite larger, rectangular, anterior corner narrowly prolonged.

Pronotum broad, almost flat, dark brown with grayish pubescence; short row of erect hairs anteriorly, raised crest in center accentuated by furrow behind, flanked by dark spot on either side; pretergite pale yellow. Mesonotum black, smooth, with whitish yellow pubescence; pubescence thicker along 2 longitudinal furrows, lighter along narrow mid-line; mesonotal suture curved, polished brown, extending to longitudinal furrows; scutum black, pubescent; scutal suture obliterated basally; scutellum brown, pubescent, finely pitted, with 2 larger pits anteriorly; postscutellum light yellow, smooth, with narrow ridge along mid-line; pleurites with minute white hairs, no discernible suture between the anepisternum and postepisternum; pleurotergal suture also lacking.

Coxae, trochanters pale; femora, tibiae, tarsi uniformly darker brown, heavily haired; tibial spurs stout, sharply pointed, covered with appressed hairs, tips bare and black; tarsal claws sharply curved, brown with black tips. Halteres with light brown knobs, stems lighter, edged with hairs.

Wings (Figs. 53, 54) strongly suffused with brown, stigma prominent, oval; Sc_1 fading out before reaching stigma; Sc_1+Sc_{2A} usually reaching radius, presence of Sc_{2B} variable; 3 branches of radius reaching margin: R_{1+2}, R_3 and R_{4+5}; r-m present, or occasionally almost obliterated; 3 branches of media reaching margin: M_{1+2} branching just beyond discal cell, therefore cell M_1 petiolate, single crossvein closing cell distally; M_{3+4} not branching, curving slightly at margin.

Abdomen brown, with darker median longitudinal streak on dorsum and venter. Terminalia of male (Figs. 4, 16): Eighth tergum entire; ninth tergum with round medial notch; basistyles with narrow fingerlike projections laterally; dististyles mostly hairy, bare at tips, longitudinal central ridge broader distally, small sclerotized lobe and notch on outer edge, broad concavity basally, aedeagus with three long slender tubes, each enclosing ejaculatory duct, tubes narrowed at tips, close together, outer pair more curved and slightly shorter than median tube; 1 small basal sclerite enveloping semen pump region of aedeagus; paraphyses (not shown in figure) long, curved, arms attached to inner sclerotized edges of basistyles; fleshy anal segment often visible in dried specimens.

FEMALE: As in male except for following characters: antennae shorter (2.5mm), dark brown, scape cylindrical; flagellar segments small, subcylindrical; covered with minute hairs, several longer hairs on each segment, shorter, stiffer ones ventrally. Terminalia (Fig. 25): Ninth tergum broad; tenth tergum large with 3 distal extensions plus a small sclerite between cercal bases; cerci broad, entire; hypovalves deeply notched distally, fused with broader eighth sternum, thin projection distally on dorsal edge.

Larva: Distinctly greenish when alive. "Body covered with numerous, elongate, trachea-bearing filaments, the posterior pair on dorsal segments deeply forked, the others simple. Spiracular disk with dorsal pair of lobes formed by rudimentary posterior branch of branched filaments of eighth abdominal segments" (Alexander, 1927a).

Pupa: "[Mesonotal] breathing horns long, almost straight. Dorsal abdominal segments with tubercles, those of sixth and eighth segments enlarged into spinous hooks; 2 pointed tubercles on seventh sternite" (Alexander, 1927a).

More complete descriptions of larvae and pupae are given by Alexander (1920).

Ecology: Rogers (1942) reports this species is "locally common to abundant about the moss and *Myriophyllum* choked pools of unshaded seepage marshes". They are often taken around the "margins of grass-sedge-fern marshes" but never found in association with *Sphagnum*.

Flight records: 12 May-30 June.

Distribution (Fig. 79): MASSACHUSETTS: Berkshire Co., Mt. Greylock, 15 June. MICHIGAN: Livingston Co., E. S. George Reserve, Honey Creek, Putnam Twp., 12-20 May; Oscoda Co., 18 June. NEW YORK: Cayuga Co., North Fairhaven, 17 May. ONTARIO: Thunder Bay Co., Nipigon, 17 June; Cochrane Co., Fort Albany (James Bay), 10 June. PENNSYLVANIA: Luzerne Co., Hazleton, 30 June. QUEBEC: Huntingdon Co., Hemmingford, 23-27 June.

Types: *P. neoxena* Alexander. Male holotype, Nipigon, Thunder Bay County, Ontario, 17 June 1913 (Dr. E. M. Walker). Female allotype and one male paratype no. 1 same data as holotype; no. 2, male, type locality, 18 June 1913; no. 3, female, North Fairhaven, Cayuga Co., N. Y., 17 May 1913. (Type and paratype no. 1 in University of Toronto collection; paratype no. 2 in C. P. Alexander collection, Amherst, Massachusetts.)

Phalacrocera tipulina Osten Sacken

(Figs. 5, 15, 24, 34-36, 43, 55, 56, 67-69, 80)

Phalacrocera tipulina Osten Sacken, 1865: 241-242; Needham, 1908: pl. 11, fig. 2 (wing); Alexander, 1914a: pl. 25, fig. 11 (wing); 1919: pl. 30, fig. 8 (wing), text fig. 125 J (male antenna); 1920: 961; 1942: 293; Dickinson, 1932: 210, fig. 112 (wing).

Diagnosis: This species is dark brown to black with a tawny pubescence. The pronotum is broad, flat and glabrous. Two branches of the radius and 3 branches of the media reach the wing margin. The 3 long, slender aedeagal tubes are readily visible, the median tube arched over the parallel lateral tubes, with the tips of all 3 converging.

Description: MALE: Body length 10-14 mm; wing length 8-11 mm. Head dorsally dark brown to black, with tawny pubescence, several light hairs posteriorly; dorsal profile triangular, narrow "neck" with 2 or 3 encircling ridges, no indentation behind eyes; palpi, labial segments dark brown, hairy; labrum and surrounding membranes orange-brown, clypeus darker brown, relatively large, rectangular, distally bearded, giving appearance of short nasus, lateral expanse about half of frontal length; fronto-clypeal suture horizontal, groove-like; antennae 3.5-4.5 mm, dusky brown, bases not raised (or only slightly so); scape longest segment, cylindrical, irregularly haired, often secondarily grooved or ringed, lateral teeth narrow (Fig. 34); pedicel globular, pubescent, with several long scattered hairs; flagellum (Fig. 35) slightly narrower than scape, segments sub-cylindrical, covered with short dense hairs, whorl of longer hairs on slight proximal enlargement, last segment attenuated medially, 4 hairs at tip; first cervical sclerite brown, small, narrow; second cervical sclerite large, rectangular, anterior corner medially prolonged.

Pronotum broad, flat, narrowed anteriorly, shiny brown except for narrow band of pubescence anteriorly before shallow groove; more distinct groove before paler pretergites. Mesonotum black with yellowish pubescence, pubescence thickest on longitudinal furrows, narrow bare line often dividing mesonotum longitudinally; mesonotal suture a polished brown shallow curve widening to shiny brown pits at longitudinal furrows; scutum black, pubescent; scutal suture indistinct or absent; scutellum brown, pubescent, with 2 pits anteriorly; postscutellum smooth, brown, whitish pubescence medially; pleurites brown, thickly pubescent, suture present between anepisternum and postepisternum; pleurotergal suture lacking.

Coxae, trochanters light brown; femora, tibiae, tarsi darker, thickest and darkest apically, covered with hairs; tibial spurs long, diverging, with short appressed hairs, bare at tips; last tarsal segment concave ventrally (Fig. 43); tarsal claws almost length of preceding segment, slender, strongly curved, several short teeth basally. Halteres brown at knobs, stems lighter, edged with hairs.

Wings (Figs. 55, 56) strongly suffused with brown, stigma darker, oval; Sc_1 fading out before stigma, Sc_{2A} present, Sc_{2B} variable; 2 branches of radius reaching costa, R_3 and R_{4+5}; r-m always present, usually touching radial crossvein and joining media close to proximal end of discal cell; 3 branches of media reaching wing margin: M_{1+2} forming rectangular edge of discall cell, cell M_1 usually petiolate; M_{3+4} not dividing, curving slightly at margin.

Abdomen dark brown, segments edged distally by darker band next to outer colorless band. Terminalia of male (Figs. 5, 15): Eighth tergum entire; ninth tergum rectangular, with narrow medial notch (smaller than in *replicata*); basistyles without lateral projections; dististyles haired at least basally, bare at tips, slender, curved and tapering distally; aedeagus with 3 long narrow tapered tubes, each enclosing ejaculatory duct, median tube arched over parallel lateral tubes, sclerotized bifurcate projection at juncture of three tubes; large basal sclerite enveloping basal half of aedeagus; paraphyses (Fig. 5), triangular plates dorsal to aedeagus.

FEMALE: As in male except for following characters: antennae (Fig. 36) considerably shorter than in male (2-2.5 mm), flagellar segments shorter, basal enlargement more pronounced, short hairs less dense; tarsal claws shorter, broader basally not strongly curved, lacking teeth. Abdomen broader than in male. Terminalia (Fig. 24): Ninth tergum a narrow sclerotized ring; tenth tergum of 4 sections: large sclerite with 3 short distal extensions, 2 small triangular sclerites in membrane between extensions, small narrow sclerite between and just anterior to cercal bases; cerci short, broad, with rounded caudal edges, smooth lateral edges; hypovalves weakly sclerotized, deeply notched at tip, thin projection distally on dorsal edge.

Variation: The tip of R_{1+2} is occasionally present on one or both wings, confusing this species with *P. replicata.* A pair of slender horny outgrowths of the pronotum were found on two specimens of approximately 300 studied. Another specimen had only one horn with no indication of its mate on the other side of the pronotum. This is probably nothing more than an anomaly.

Larva: Not seen.

Pupa (Figs. 67-69): Only pupal skins were available for study. Specimens were light brown, wing pads and leg sheaths darker, darker brown stripe on dorsal mid-line, pair of small spots laterally on venter of each segment.

Length 13.5 mm; width 3 mm. Cephalic part of head broad, without spines or lobes. Prothorax lacking processes. Mesothorax broad, irregular, with a slender pair of curved breathing horns anteriorly, devoid of other processes. Broad wing sheaths extending down two-thirds of second abdominal segment. Metanotum devoid of spines; haltere sheaths lying alongside first abdominal segment, partially covered by wing sheaths. Leg sheaths extending almost to end of third abdominal sternum. First abdominal segment short, without processes. Abdominal segments 2 to 8 as follows: 4 pairs of spots dorsally, posterior 2 bearing short hair on small prominence; ventrally (Fig. 68) with 2 oval spots antero-laterally, 3 pairs of tiny spots medially, a thin transverse division behind which lies a roundish spot on each side of mid-line, and more posteriorly, a pair of small spines on each side; laterally produced into a broadly bi-lobed flange, a pigmented spot at each tip. Eighth segment with a broad lateral flange, a small pigmented spot at broadest portion on each side; 4 small spines ventrally, middle 2 larger; posteriorly, 2 rounded processes, each tipped with a small hair. Ninth segment terminating in several lobes: dorsal pair of lobes longest, 2 rows of spines dorsally; 6 ventral lobes, middle lobe smallest; deeply bilobed lateral process, outermost lobes broader, tipped with 3 small hairs.

This pupa is quite similar to that of *P. replicata,* differing only in the absence of a pair of terminal processes on the dorsum of the sixth abdominal segment and on the seventh abdominal sternum.

Ecology: This species is not as difficult to find as are most Cylindrotominae. It occurs in or near sphagnum bogs in northern or mountainous locali-

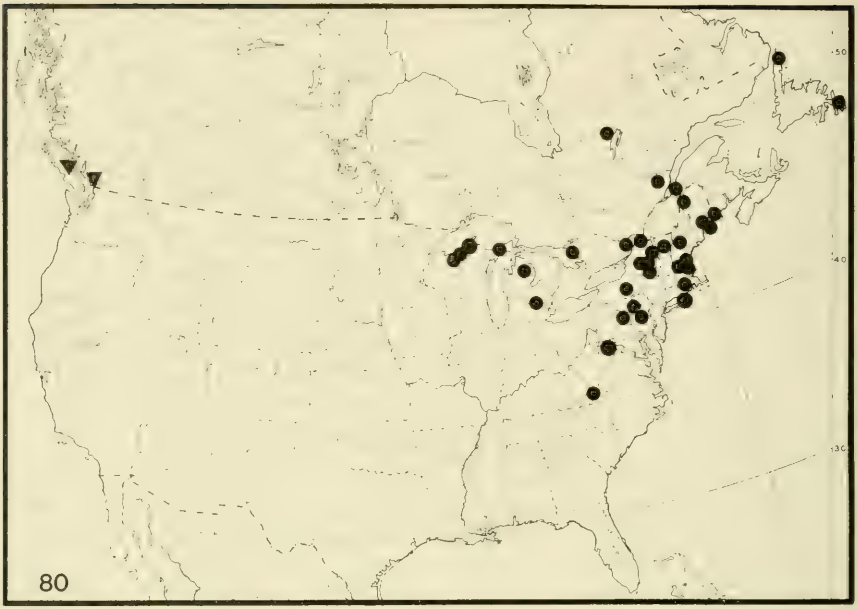

Fig. 80. Ranges of *Phalacrocera vancouverensis* (inverted triangles) and *Phalacrocera tipulina* (circles). Each spot represents one or more collections within a county or at a locality.

ties. Good series have been taken in Michigan (J. S. Rogers) and Pennsylvania (G. W. Byers). Byers recorded in his field notes (Centre County, Pennsylvania) taking these flies "in low-hanging branches of alder and hemlock along the edges of a marsh and in clumps of *Carex*. Several mating pairs were collected. The female supports or suspends the male or both may cling to adjacent leaves of *Carex* for support. The flies hang up with wings outspread and may let hind legs hang free." A live male pupa and several male skins were found in low hummocks of *Sphagnum*. Wing remains of this species have been found in the pitcher plant, *Sarracenia purpurea* (see Alexander, 1920).

Flight records: 9 May-6 Sept.

Distribution (Fig. 80): CONNECTICUT: Windham Co., Putnam, 15 June; (?) Co., Manitic Lake, 8-9 June. MAINE: Aroostook Co., Ninemile (near Lac Frontière, Quebec), 2 June; Hancock Co., Bar Harbor, Mt. Desert, 4-23 July; Penobscot Co., Bangor, May-July; Washington Co., Machias, May-July. MARYLAND: Garrett Co., Cranesville Pine Swamp, 18 June. MASSACHUSETTS: Essex Co., Beverly, 3 June. MICHIGAN: Gogebic Co., 15 June-16 Aug.; Houghton Co., 20 June; Livingston Co., 12 May; Oscoda Co., 19-25 June; Schoolcraft Co., Floodwood, 20 July-14 Aug. NEWFOUNDLAND: Avalon Peninsula, Cochrane Pond (450 ft.), Mackinson's, St. John's (Karwood Cabins, along shore of Neville's Pond), Cataracts of North Harbor River near Colinet, 22-30 June; White Bay District, St. Anthony, 2 July. NEW HAMPSHIRE: Cheshire Co., Mt. Monadnock area, May-July; Coos Co., White Mountains, May-July; Rockingham Co., Hampton area, May-July. NEW YORK: Essex Co., Ausable Lakes, Hampton, Lake Tear of the Clouds, Mt. Marcy, 10-30 July; Fulton Co., near Sacandaga Park, Canada Lake (1600 ft.), 18 June-10 July; Hamilton Co., Lake Pleasant, 20-21 June; Herkimer Co., Old Forge, July-3 Aug.; Suffolk Co., Riverhead, 2 June; Tompkins Co., Ringwood Hollow, 3 July. ONTARIO: Carlton Co., Mer Bleu, Hawthorne, Ottawa, 20 May-6 Sept.; Georgian Bay, 13 July. PENNSYLVANIA: Centre Co., Bear Meadows (1820 ft.), 25-26 June; Luzerne Co., Hazelton, 19 May-4 June; Sullivan Co., 27 June. QUEBEC: Huntingdon Co., Covey Hill, Hemmingford, 27 June-13 July; Kamouraska Co., Andreville, 25-31 June; Laurentides Park, 24 June-16 Aug.; large bog 2 mi. N Lake Mistassini, Rupert River, 10 June-13 July. VERMONT: Lamouille Co., Stowe, 24 June. VIRGINIA: Giles Co., Hawthorne, Little Stoney Creek, Mountain Lake, 29 May-21 June. WISCONSIN: Vilas Co., July.

Types: Two syntypes (male and female), White Mountains, New Hampshire. (no. 10238, Museum of Comparative Zoology, Harvard University.)

Phalacrocera vancouverensis Alexander

(Figs. 6, 18, 38, 44, 57, 58, 80)

Phalacrocera vancouverensis Alexander, 1927b: 189-190; Spencer: 1930: 15-16.

Diagnosis: This species is dark brown and robust, with whitish pubescence on the head and golden pubescence on the thorax. The pronotum has a prominent transverse crest. Three branches of the radius and 3 of the media reach the wing margin. The flagellar segments have verticils. The mesonotal suture is narrow, dull and darker than the rest of the thorax.

Description: MALE: Body length 12-13 mm; wing length 10-12.6 mm. Head dark brown to black, with whitish pollinosity of short hairs, most dense ventrally and around eyes, several brown hairs on vertex; dorsal profile of head broadly rectangular, with short narrow "neck" region; labium, labrum, and palpi brown, membranes yellowish; clypeus large, trapezoidal, brown-black, with whitish pubescence, several brown hairs distally, lateral extensions narrow; fronto-clypeal suture broad, horizontal (not as well defined as in *tipulina*); antennae dark brown, scape longest segment, cylindrical, bearing scattered hairs, lateral tooth obscured on available specimens; pedicel globular, with scattered hairs; flagellar segments (Fig. 38) subglobular, slightly longer than pedicel, slightly produced ventrally, bare except for whorl of short dark hairs on each segment; first cervical sclerite brown, small, narrow; second large, rectangular, its curved edge without narrow anterior prolongation.

Pronotum dusky black, broad, with prominent transverse crest, bordered anteriorly with erect hairs; pretergites brown. Mesonotum dull black, with golden pubescence; longitudinal furrows barely suggested by slightly heavier pubescence, no median longitudinal line on thorax; mesonotal suture dull brown, narrow, slightly curved, visible only behind median stripe of thorax; scutum dark brown; scutal suture distinct; postscutellum and pleurites dull brown with light grayish pollinosity, membranes dusky beige; suture present between anepisternum and postepisternum; pleural suture lacking.

Coxae, trochanters obscure yellow; femora brownish yellow, lighter basally, tips widened and dark brown; tibiae, basitarsi light brown, tips narrowly darkened; other segments of tarsi dark brown; tibial spurs lighter brown, black tipped, conspicuous; tarsal claws (Fig. 44) sharply curved, with small bump near broad base. Knobs of halteres dark brown, stems dusky yellow, haired.

Wings (Figs. 57, 58) strongly suffused with brown, stigma barely discernible; Sc_1 fading out before stigma, no evidence of Sc_2; 3 branches of radius reeaching costa: R_{1+2}, R_3, R_{4+5}; R_{1+2} very short, sharply diverging from R_3; r-m in line with base of discal cell; 3 branches of media reaching margin: M_{1+2} branching just beyond edge of discal cell, cell M_1 petiolate. M_{3+4} not branching, slightly curved at margin.

Abdomen dark brown, segments edged distally by narrow colorless bands. Terminalia (Figs. 6, 18): Character of eighth and ninth terga obscured in specimen examined (on slide). Dististyles irregularly shaped, with flat rounded head, a notch and a small tooth along inner edge, several small teeth along outer of broad basal region; 3 tubes of aedeagus on same plane, outer two curved, inner straight, each narrowed distally; basal sclerites "H-shaped," lying dorsal to aedeagus; paraphyses long, narrow sclerites attached to inner sclerotized edges of basistyles (not shown in figure). Holotype differs in the following characters: antennae slightly shorter than in male, scape and flagellar segments oval to subcylindrical, not produced at all ventrally nor truncate apically; last segment elongate, nearly twice length of penultimate; each segment with a whorl of hairs; terminal segment elongate, relatively long, conspicuous. Wing of holotype possesses r-m crossvein. (Probably this character is quite variable in *vancouverensis.*) Abdomen light yellowish brown, with conspicuous black median stripe on dorsum and venter; first segment darkened, pruinose; caudal margins of segments narrowly pale. Terminalia (observations incomplete due to insufficient material): Base of cerci obscured by rather large, distally pointed hairy tenth tergum. Tips of cerci subacute, caudal margins roughened, almost serratulate. Hypovalves deeply notched.

Immature stages: Not seen. The larva is bright green and has bifurcated filamentous dorsal and lateral processes (Spencer, 1930).

Ecology: Spencer (1930) observed that the larva was green and resembled the stems of the pond weed *Nitella,* to which it was clinging. Its movements were sluggish, barely perceptible. The long bifurcated dorsal and lateral "gills" were very slowly waved back and forth. After pupation, the last laval skin remained loosely attached to the pond weed and the pupa floated at an angle of 30° to the water surface.

Flight records: 10 April-9 Aug.

Distribution (Fig. 80): BRITISH COLUMBIA: Vancouver Island, Forbidden Plateau, 9 Aug.; Vancouver District., Vancouver, 10 April.

Type: Female holotype, Vancouver, 10 April 1922 (W. B. Anderson), in (Canadian Nat. Collection). Male allotype (genitalia on slide), Forbidden Plateau, Vancouver, British Columbia, 9 Aug. 1950; (in Museum of Zoology, University of Michigan, Ann Arbor).

Liogma Osten Sacken

Liogma Osten Sacken, 1869: 298; Peus, 1952: 66.
Type: Triogma nodicornis Osten Sacken.

Liogma is a poorly defined genus represented by only one species in North America. It shows many striking similarities to *Triogma* in wing venation and genitalia, yet superficially these genera are quite dissimilar.

Diagnosis: This genus is distinguished by having strongly nodulose, almost cordate antennal segments which are much more pronounced in the male than in the female. The prescutal stripes are shiny black.

Description: Head shiny black, with fine light hairs laterally and posteriorly; scape long, cylindrical; flagellar segments nodulose or cordate; pronotum bare; pretergites pale yellow; prescutum pale yellow with 3 shiny black stripes; mesonotal suture a shiny brown curve ending in small pits on either side of median stripe; scutum divided longitudinally by distinct suture; scutellar sutures obscured in dark brown, spindle-shaped pits; pleural sclerites pale yellow, brown-black areas on anepisternum, postepisternum; pleurotergite brown-black, wrinkled; wings suffused with brown, stigma oval, very pale; Sc_1 fading before stigma; Sc_{2A} present, Sc_{2B} obliterated; 2 branches of radius reaching margin (R_3 and R_{4+5}); r-m obliterated by fusion of R_{4+5} with M_{1+2} at corner of or before discal cell; 3 branches of media reaching wing margin (M_{1+2}, M_3, M_4); medial crossvein plus part of M_3 closing discal cell distally; tibial spurs very short, stout, haired; tarsal claws long, slender, broadly curved. Abdomen dark brown, distal edge of each segment colorless.

male terminalia: Eighth tergum entire; ninth tergum squarish, produced into 2 conical projections distally; aedeagus with 3 tubes each enclosing ejaculatory duct leading from semen pump.

female terminalia: Ninth tergum very narrow; tenth tergum divided into 4 sclerites: large median sclerite, pair of triangular lateral sclerites, one narrow anterior sclerite; cerci short, broad, not distinctly serrate.

Liogma nodicornis (Osten Sacken)

(Figs. 7, 19, 26, 39, 40, 59-62, 74, 81)

Triogma nodicornis Osten Sacken, 1865: 239-240.
Cylindrotoma nodicornis Osten Sacken, 1869: 301.
Liogma nodicornis Osten Sacken, 1869: 298; Alexander, 1914b: 105-118; 1927a: 10-11.
Liogma nodicornis flaveola Alexander, 1919b: 195.

Diagnosis: This species is intermediate in length between *Cylindrotoma* and *Phalacrocera*. The thorax is pale yellow with shiny black or dark brown stripes. The antennal segments are strongly nodulose or cordate.

Description: male: Body length 9-12 mm; wing length 8.5-9.5 mm. Head shiny black, broadly oval, tapering behind eyes; labium, labrum medium brown, haired distally; palpi darker brown; membranous areas tawny; clypeus dark brown, short, narrow, convex, with long hairs distally extending over labial segments; fronto-clypeal suture arched; antennal bases close together, separated by narrow incision-like groove; scape long, cylindrical, slightly narrower than flagellum and roughly twice the length of 1 flagellar segment, bearing several hairs; lateral teeth not pronounced; pedicel subovate; most flagellar segments expanded ventrally (Fig. 39), distal segments sub-ovate, last segment attenuated, slender; dense, erect, short hairs covering each flagellar segment, verticillate, dorsal bristles longer.

Pronotum pale yellow to dark brown in center, anterior region reduced, prominent narrow transverse crest near mid-length; pretergites pale yellow with short erect hairs; prescutal stripes shiny black, median stripe divided posteriorly by short narrow longitudinal furrow; scutellum light brown; postscutellum shiny brown posteriorly, paler and wrinkled anteriorly. Halteres dusky, lighter at base of stem; thick row of hairs on anterior edge.

Coxae brown, trochanters light yellow, edged with black; femora, tibiae very pale, brown at tips, covered with short, stout hairs, each in small brown spot; tarsi dark brown, hairs long.

Terminalia (Figs. 7, 19): Dististyles light brown, slender, widened at base, covered with short hairs except for bare tips, denser hairs along inner edges; aedeagus branching into three tubes beyond junction of ejaculatory ducts, outer tubes slightly more curved than median tube; ventral side of each tube prolonged distally, tips flattened; basal sclerite apparently fused to aedeagus and joined to paraphyses by a long narrow extension on each side; paraphyses irregular sclerites (Fig. 7) lying dorsal to aedeagus; anal segment lightly sclerotized.

FEMALE: Differs from male in the following: antennae (Fig. 40) somewhat shorter, pedicel and flagellar segments nodulose, not cordate, verticils shorter than in male. Terminalia (Fig. 26): Large median sclerite of tenth tergum with three sharp points on caudal margin. Cerci with very small irregular terminal teeth; hypovalves short, broadly notched distally, fused to slightly broader eighth sternum.

Variation: Considerable variation has been noted in the extent of color on the mesothorax. The black mesonotal stripes may merge anteriorly or be distinct along their entire length. The background color varies from very pale to quite dusky yellow. Pleural sclerites and postnotum are very pale in some specimens. Wing variations include the occasional presence of r-m, occasional absence of Sc_{2A} and m-cu joining M before, beyond or at the base of the discal cell. One specimen was found with an additional crossvein in cell R_5 (Fig. 62).

Larva: Living specimens are light green. Numerous slender lobes covering body are darker. Preserved specimens are pale whitish-yellow with dark oblique marks laterally on abdominal segments. Tuberculate paired processes on abdominal terga each bearing a small sharp tooth anteriorly near base.

Pupa: Living pupae are light yellow to brown (probably depending upon age). Preserved specimens are brownish with an interrupted dark longitudinal line along either side of the middle of the dorsum. Each abdominal segment bears a single dorsal pair of slender lobes.

Detailed descriptions of the immature stages are presented by Alexander (1914).

Ecology: The adults of this species are relatively abundant although quite local in distribution. They are very sluggish flyers and may be swept from rank vegetation in cool, shaded, or partially shaded woodlands, in tamarack and sumac swamps, and along wooded margins of marshes. The Alberta specimens were collected at the edge of spruce and tamarack "muskeg" (Alexander, 1927c). Immature stages of these flies have been found feeding on *Mnium punctatum, Hypnum cupressiforme* and related species of mosses, and in shallow pools.

Flight records: 7 May-28 July.

Distribution (Fig. 81): ALBERTA: Bilby (30 mi. W. of Edmonton), 19 June. CONNECTICUT: Fairfield Co., Redding, 2 June; Hartford Co., Grandby, W. Grandby, Hartland, 8-9 June; Litchfield Co., Cornwall Bridge, Kent Falls, Norfolk, Riverton, 31 May-13 June; New Haven Co., Hamden, 2 June. DISTRICT OF COLUMBIA: Washington (no date). GEORGIA: Union Co., Neel Gap, 22 May. ILLINOIS: Carroll Co., Savanna, 15 June. INDIANA: Jefferson Co., 25-27 May; Owen Co., McCormick's Creek State Park, 6 June; Parke Co., Turkey Run State Park, 28 May-11 June. MAINE: Franklin Co., Rangeley Lakes, June-July; Hancock Co., Mt. Desert area, 7 June-4 July; Penobscot Co., Bangor, Ellsworth, Orono, 8 June-July; Piscataquis Co., Capens (Moosehead Lake area), June-July; Washington Co., Machias, 25 July. MANITOBA: Portage la Prairie Distr., Aweme, 25 May-16 June; Souris Distr., Ninette, 12 June. MARYLAND: Montgomery Co., Glen Echo; Prince Georges Co., Beltsville, Bowie, 29-31 May. MASSACHUSETTS: Berkshire Co., Mt. Greylock, N. Adams, 14-18 June; Hampshire Co., Amherst, 3-16 June; Worcester Co., Petersham, June. MICHIGAN: Clinton Co., Beulah, Cusino, Rose Lake, 24 May-27 June; Crawford Co., 4 June; Delta Co., 11 June; Ionia Co., Ionia, 31 May; Iron Co., 13 June; Keweenaw Co., Copper Harbor, 19 June; Houghton Co., 20 June; Lake Co., 8 June; Livingston Co., E. S. George Reserve, 26 May-27 June; Mackinac Co., 7 June-5 July; Marquette Co., Huron Mts., 13-15 June; Newaygo Co., 21 July; Oakland Co., 20 May; Ogemaw Co., Rifle River area, 3-10 June; Ontonogon Co., 18 June; Oscoda Co., 14-15 June; Roscommon Co., 4 June; Schoolcraft Co., 8 June-5 July; Washtenaw Co., Ann Arbor, Cascade Glen, 28 May-10 June. MINNESOTA: St. Louis Co., Eagle Nest, 4 June. NEW BRUNSWICK: Charlotte Co., Waweig, 23 May. NEWFOUNDLAND: Bonavista North and Bonavista South Distrs., Middle Brook, Southwest River near Lethbridge, Terra Nova Nat'l Pk., 3-6 July. NEW HAMPSHIRE: Cheshire Co., Jaffrey, Mt. Monadnock, 19 June; Coos Co., Bretton Woods, Randolph, White Mountains, May-July; Grafton Co., Franconia, Hanover, June-July. NEW JERSEY: Essex Co., Orange Mts., West Orange, June; (?) Co., Hemlock Falls, May. NEW YORK: Erie Co., Hamburg, 28 May-20 June; Essex Co., Mt. Marcy, Heart Lake (2150 ft.), 29 June; Fulton Co., Canada Lake, Gloversville, Johnstown, Sacandaga Park, Vanderburgs, 15-27 June; Hamilton Co., Lake Pleasant, 20 June; Herkimer Co., Indian Castle, 9 June; Onondaga Co., Green Lake; Orange Co., Bear Mt., 31 May; Brookview, 7 June; Tompkins Co., North Lansing, Ithaca, 1-14 June; Washington Co., Hampton (no date); Westchester Co., Dobbs Ferry, Tarrytown, 9 June; (?) Co., Misake, 20 June. NORTH CAROLINA: Buncombe Co., Swannanoa, 23 May; Burke Co., Linville Falls (3250 ft.), 3-10 June; Haywood Co., Black Mt., Mt. Pisgah (3000 ft.), 28 May; Jackson Co., Cashiers (3800 ft.), 12 June; Macon Co., Highlands (4000 ft.), Van Hook Glade (3800 ft.), Nantahala Gorge, May-June; Swain Co., Great Smoky Mountains National Park, Forney Ridge trail (6000-6300 ft.), 18 June; Transylvania Co., Camp Toxoway (3200 ft.), 9-10 June; Wake Co., Raleigh, May; Yancey Co., Mt. Mitchell Game Refuge (3100 ft.), 22 May-9 June; (?) Co., Conestee Falls, 12 June. NOVA SCOTIA: Kings Co., Kentville, 4 July; Victoria Co., Baddeck, 6-27 July. OHIO: Hocking Co., Goodhope Twp., 20 May-6 June, Wayne Co., Wooster, 13 May. ONTARIO: Carleton Co., Britannia Bay, Ottawa, 1-12 June; Cochrane Co., Fort Albany (James Bay), 15-19 June; Kent Co., Bothwell, 13 June;

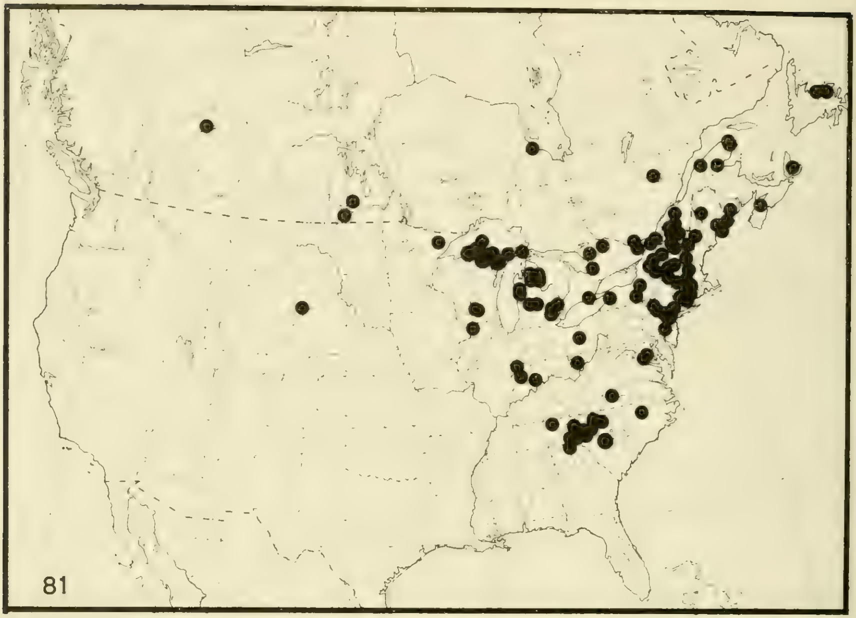

Fig. 81. Range of *Liogma nodicornis*. Each spot represents one or more collections within a county or at a locality.

Nipissing Co., Algonquin Pk., 3 June-7 July; Norfolk Co., Normandale, Simcoe, 9-20 June; Parry Sound Co., Burks Falls, Kearney, Sand Lake, 29 June-16 July; Simcoe Co., Orillia, 28 June-2 July; (?) Co., Fishers Glen, 2 July. PENNSYLVANIA: Carbon Co., Palmerton, 10 June; Luzerne Co., Hazleton, 22 May-26 June; Philadelphia Co., Roxborough, 7 June. QUEBEC: Bonaventure Co., Escuminac, 2-31 July; Brome Co., Knowlton, 14-29 June; Gaspé East Co., Gaspé, 26 June-28 July; Gaspé West Co., Anse Pleureuse, Mt. Lyall (1500 ft.). 27 June-29 July; Gatineau Co., Hull, Meach Lake, 28 May-21 June; Huntingdon Co., Covey Hill, 17 June; Lake St. John West Co., Mistassini, (?) June-20 July; Matane Co., Metis-sur-mer, 26 June-29 July; Megantic Co., 6-16 July; Richmond Co., Stoke Centre, 26 June; Shefford Co., Abbotsford, 17 June; Stanstead Co., Georgeville, 14-19 June; Terrebonne Co., Montreal, (?) June. SOUTH CAROLINA: Spartanburg Co., Spartanburg, 13 May. SOUTH DAKOTA: Pennington Co., Harney Peak (6700 ft.), 15 July. TENNESSEE: Great Smoky Mountains National Park, Siler's trail (6000-6500 ft.), Indian Gap (5300-5500 ft.), Anakeesta Ridge (4500 ft.), Leconte Lodge (6400 ft.), Greenbrier, Brushy Mt. trail (3500 ft.), 7 May-15 June; Green Co., Camp Creek, 7 May; Scott Co., 29 May. VERMONT: Bennington Co., Manchester, 6 June; Franklin Co., St. Albans, 19 June; Washington Co., Montpelier, 25 June. VIRGINIA: Alexandria Co., Glencarlyn, 7 June; Arlington Co., Chain Bridge, 28 May; Fairfax Co., Dead Run, Falls Church, Great Falls, 19 May-18 June; Giles Co., Kire, Little Stoney Creek, Mountain Lake, 27 May-17 June. WISCONSIN: Dane Co., May-June; Sauk Co., 28 May.

Types: 8 syntypes (5 males, 1 female, 2 broken), Washington, D. C., Dobbs Ferry, New York; White Mountains, New Hampshire; Illinois; New Jersey (no. 10236, Museum of Comparative Zoology, Harvard University). One male paratype, New Jersey, May (in Academy of Natural Sciences of Philadelphia).

Liogma nodicornis flaveola Alexander, male holotype, Great Falls, Virginia, 19 May 1915; allotype, Great Falls, Virginia, 7 June 1915 (in C. P. Alexander collection, Amherst, Massachusetts).

Triogma Schiner

Triogma Schiner, 1863: 223; Osten Sacken, 1865: 237-241.
Type: Limnobia trisulcata Schummel.

This is a very small genus consisting of four known species with only one from North America. Peus (1952) places the two Oriental species of *Triogma* (*nimbipennis* Alexander, *kuwanai* Alexander) "incertae sedis" pending more detailed studies, particularly of the genitalia. Thus this genus is actually based on only two species (*trisulcata* of Europe and *exsculpta* of North America).

Diagnosis: A heavily rugose and pitted head and thorax and dull dark coloration distinguishes this genus in North America.

Description: Head bare, dull dark brown, pitted; scape long, cylindrical; flagellar segments subcylindrical; pronotum bare; pretergites glabrous, dark brown; prescutum concolorous dark brown to black, two longitudinal series of pits trisecting mesothorax; mesonotal suture pitted, ending at and joining with longitudinal rows of pits; scutal suture pitted; scutellar sutures obscured by two deep pits; all pleural sclerites dark brown to black, pitted; wings strongly suffused with brown, stigma absent; Sc_1 extending to juncture of Sc_{2A} with radius; Sc_{2B} usually present; 2 branches of radius reaching margin (R_3 and R_{4+5}); r-m usually obliterated by short fusion of R_{4+5} with M_{1+2} at corner of discal cell; three branches of media reaching wing margin: M_{1+2} not dividing, forming basal and anterior edges of discal cell; M_{3+4} at posterior edge of cell, branching, M_3 and M_4 attaining margin independently; medial crossvein plus part of M_3 closing cell distally; tibial spurs short, prominent, haired; tarsal claws short, broad, abruptly curved distally. Abdomen dull dark brown, posterior edge of each segment pale.

MALE terminalia: Eighth tergum entire; ninth tergum squarish, 2 small broad caudal projections laterally; aedeagus with 3 tubes, each enclosing an ejaculatory duct leading from semen pump.

FEMALE terminalia: Ninth tergum very narrow; tenth tergum divided into four sclerites: large median pentagonal sclerite, 2 small triangular sclerites, 1 on each side, one narrow anterior sclerite; cerci short, broad, not serrate.

Triogma exsculpta Osten Sacken

(Figs. 8, 20, 27, 41, 42, 63-66, 70-73, 75, 76, 82)

Triogma exsculpta Osten Sacken, 1865: 239; 1869: 304-305.
Triogma exculpta [sic]; Alexander, 1919: 926; 1920: 974; 1927: 11; 1942: 296; Rogers, 1942: 77.

Diagnosis: *Triogma exsculpta* is the stockiest and darkest species in this subfamily. It is dull dark brown to black with characteristic pits or punctations on both the head and the thorax.

Description: MALE: Body length 7-8 mm; wing length 7-8 mm. Head dull dark brown, subspherical, rugose; labium, palpi dark brown, haired;

labrum dark brown, glabrous; membranes around mouth parts dusky; clypeus very short, dark, convex, not extended laterally, with small hairs distally; fronto-clypeal suture arched; antennal bases very close together; scape cylindrical, longest and broadest segment, sparsely haired, bearing small tooth on each side, inner tooth broader than outer tooth; pedicel subglobular, sparsely haired; flagellar segments subcylindrical, covered with long erect hairs, verticils in an uneven whorl.

Pronotum dark brown to black, a shiny brown furrow separating anterior pitted ridge from shiny, lighter posterior portion; prescutum black, with tawny pubescence, trisected by 2 longitudinal rows of deep pits, a secondary row of pits along mid-line; scutum, scutellum black with tawny pubescence; postscutellum smooth, with 2 black spots posteriorly, anteriorly lighter, wrinkled, longitudinally divided by shallow furrow; pleural membranes dusky orange-brown. Stems of halteres pubescent, dusky yellow, knobs darker.

Coxae blackish, pubescent; trochanters lighter, pubescent, sparsely haired; femora, tibiae, tarsi light brown, haired, segments progressively more haired distally.

Terminalia (Figs. 8, 20): Dististyles short, simple, curved, haired, but tips bare; aedeagus branching into 3 tubes beyond junction of ejaculatory ducts, middle tube more curved than lateral tubes; ventral side of each tube slightly prolonged distally (less pronounced than in *Liogma*), tips flattened; basal sclerite apparently fused to aedeagus; paraphyses irregular sclerites lying dorsal to aedeagus (Fig. 8); anal segment lightly sclerotized.

FEMALE: Differs from male in the following: antennae (Fig. 42) shorter, flagellar segments subspherical, almost moniliform, hairs extremely short, verticils just below mid-length of each segment. Terminalia (Fig. 27): Cerci flat, broad, smoothly rounded, notched laterally; hypovalves short, broadly notched posteriorly, narrower than and fused to eighth sternum.

Variation: This species is quite uniform; however, variations in wing venation are found, e.g., the absence or only traces of Sc_2 and of the tip of Sc_1, occasional presence of r-m; also, the position of m-cu is quite variable, and the medial crossvein is often lacking.

Larva (Figs. 70-73): Only preserved specimens have been studied. This larva is distinguished by having short, paired tergal and sternal lobes, no distinct color pattern and 3 pairs of lobes (2 large, 1 small) surrounding spiracular disk.

Length 16 mm; width 3 mm. Head completely retractile into prothorax, the latter having neither hairs nor bristles. Numerous conical lobes cover larva. Prothorax with 2 pairs of short, simple, dorsal lobes, anterior pair smaller and closer together than posterior pair; 1 pair of lateral lobes; no ventral lobes. Mesothorax with 2 pairs of dorsal lobes, posterior pair slightly larger, lobes with a small anterior protuberance at base; 2 pairs of simple lobes on each side. Metathorax dorsally as for mesothorax; 3 simple lobes on each side and 3 pairs of ventral lobes, second pair largest, placed further apart. Dorsal abdominal lobes as follows: first abdominal segment with 2 pairs of lobes, each with an anterior protuberance; 4 pairs of lobes on segments 2 to 7, first pair very small (largest on second segment, becoming progressively smaller towards posterior end of larva), second pair of lobes slightly larger, third pair with two dorsal tooth-like protuberances, fourth pair longest, with one dorsal "tooth". Lateral abdominal lobes simple; first abdominal segment with two on each side; second to seventh abdominal segments with 3 on each side. Ventral lobes simple, conical projections, arranged in pairs, posterior pair largest: 2 pairs on first abdominal, 5 pairs on second to seventh abdominal segments. Probably 3 or 4 segments involved in caudal region of larva. Spiracular disk (Fig. 66) small, the 2 rounded spiracles situated side by side, inclined toward each other; 3 pairs of lobes surrounding spiracle, a small median dorsal pair, a longer dorso-lateral pair, and a ventral pair with a conspicuous black line on inner surface of each lobe, tip ending in a sharp recurved hook. Ventral surface of terminal segment with protuberances (Fig. 67).

Triogma exsculpta larvae closely resemble those of *Liogma nodicornis* but differ from the latter by having no color pattern, a hairless pronotum, and an additional small pair of dorsal lobes on the spiracular disk.

Pupa (Figs. 75, 76): Only preserved female specimens have been studied. This pupa is distinguished by having no color pattern and by 2 short, dorsal pairs of lobes on each segment, each with a very small, basal protuberance.

Length 12 mm; width 3 mm. Cephalic part of head flat, broad, without lobes. Prothorax without processes. Mesonotal breathing horns small, directed dorsad and laterad, terminal half bent cephalad. Mesonotum with two small slender lobes caudally; broad wing sheaths laterally reaching posterior margin of second abdominal segment. Metanotum with 2 pairs of simple lobes, anterior pair very small, posterior pair longer; lateral haltere sheaths lying alongside first abdominal segment, obscured by wing sheaths. Leg sheaths ending just before posterior margin of third abdominal sternum. First abdominal segment short, 2 pairs of dorsal processes posteriorly, each with small sharp tooth basally; no ventral nor lateral processes. Abdominal segments 2 to 7 with 3 pairs of dorsal processes, anterior pair small, simple (not always figured, obscured by posterior pair of processes of preceding segment), middle pair longer, bearing 2 sharp spines anteriorly, posterior pair largest, 2 teeth anteriorly; laterally 3 simple lobes on each side; ventrally 3 pairs of short simple spines, anteriormost pair extremely tiny. Eighth abdominal segment smaller than seventh, terminating in lateral lobes, with a small medial pair of spines on dorsum and on venter. Ninth abdominal segment narrower than eighth,

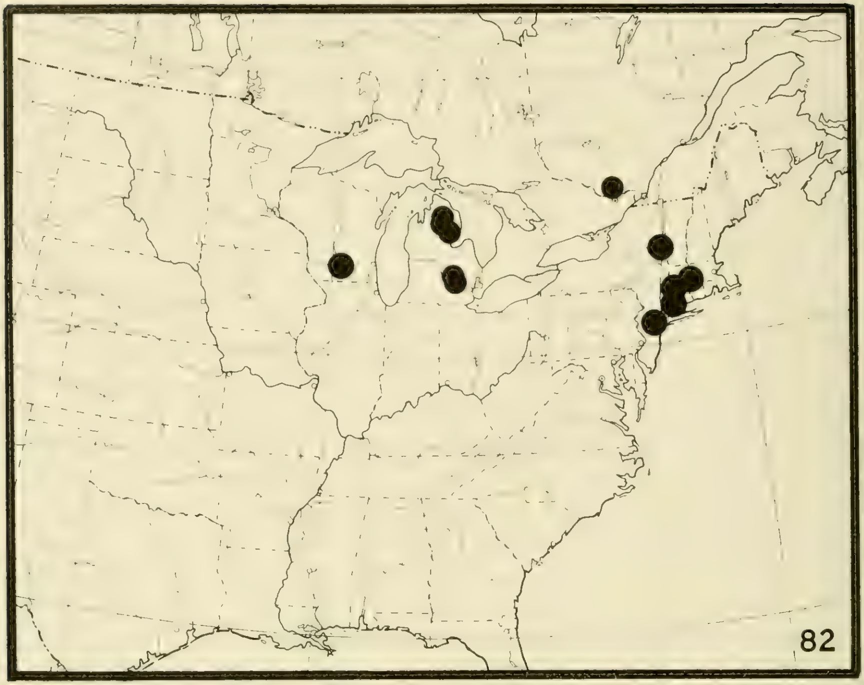

FIG. 82. Range of *Triogma exsculpta.* Each spot represents one or more collections within a county or at a locality.

terminating dorso-laterally in a pair of lobes, between which the developing female cerci can be seen in mature specimens.

This pupa closely resembles that of *Liogma nodicornis* but may be differentiated from the latter by having no dorsal pattern and by having 3 pairs of dorsal lobes on all but the first abdominal tergum.

Ecology: Rogers (1942) reported *Triogma exsculpta* as very local yet numerous in quite limited areas. The flies may be found in seepage areas and along short marshy spring rills and are often found in wet mossy meadows where there is no woody vegetation. The larvae and pupae have been collected on the aquatic moss *Fontinalis antipyretica,* and they have been found on floating mosses of small marsh pools.

Flight records: 20 April-19 June.

Distribution (Fig. 82): CONNECTICUT: Fairfield Co., Stamford, 15 May, Litchfield Co., Norfolk, 9 June. MASSACHUSETTS: Hampshire Co., Amherst, 20 April-25 May. MICHIGAN: Arenac Co., 25 May; Crawford Co., Branch of Big Creek, 23 May-19 June; Livingston Co., E. S. George Reserve, Honey Creek, Putnam Twp., 15-20 May; Otsego Co., 24 May; Washtenaw Co., 15 May. NEW HAMPSHIRE: (no further data). NEW JERSEY: Essex Co., Waverly, May. NEW YORK: Washington Co., Hampton, 20 May. PENNSYLVANIA: (no further data). QUEBEC: Gatineau Co., Hull, 17 May. WISCONSIN: Dane Co., 10 May.

Types: Female holotype, Pennsylvania, (ANSP Type no. 6058, Academy of Natural Sciences, Philadelphia).

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THE UNIVERSITY OF KANSAS
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SPERM TRANSPORT FERTILIZATION AND PREIMPLANTATION LOSS IN PHH AND PHL MICE

By

John E. Lothers, Jr.

Vol. XLVII Pages 117-144 April 14, 1967 No. 4

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THE UNIVERSITY OF KANSAS
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Sperm Transport Fertilization and Preimplantation Loss in PHH and PHL Mice[1]

By

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ABSTRACT

To investigate reasons for the smaller litters and higher sex ratio in litters sired by PHH mice compared to litters sired by males of the PHL strain, spermatozoa were subjected to a variety of treatments.

Single and mixed batches of spermatozoa were inseminated artificially. The interval between injection of PHH and PHL spermatozoa varied between 0 and 96 minutes. Preimplantation and post-implantation losses were investigated by means of ova and fetal counts along with counts of corpora lutea and resorptions. Spermatozoa from the vasa deferentia and from ejaculates were examined for numbers, morphology and percentage viability. Proportions of normal and abnormal spermatozoa reaching the oviduct following copulation by an intact male were compared with proportions found in the uterus.

Following artificial inseminations with mixtures of PHH and PHL spermatozoa, there were significantly fewer litters containing progeny from PHH than PHL spermatozoa, even when conditions were seemingly heavily weighted in favor of PHH. The competitive disadvantage of PHH spermatozoa could be partially compensated for by injecting 69 or more minutes before PHL. Hyaluronidase added to the PHH extender also seemed to compensate partially for the disadvantage and an effect of hyaluronidase on the sex ratio is indicated. *In vivo* and *in vitro* (ß-amylase) capacitation of PHH spermatozoa before insemination proved ineffective. Preimplantation losses as determined from counts of ova, fetuses, resorptions, and corpora lutea tend to be higher following copulation with PHH than PHL males. Much of the difference is attributable to a few cases in which PHH spermatozoa fertilize only a few of the available ova. There was no significant difference between strains in sperm number or morphology. However, the proportion of spermatozoa from the vas deferens that were viable was higher in PHL than PHH. There was wide fluctuation within strains in sperm counts

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from ejaculates. There was no evidence for a greater proportion of morphologically abnormal PHH than PHL spermatozoa entering the oviduct. Looped (bent) spermatozoa, found in larger proportions in PHH than in PHL ejaculates, are able to enter the oviduct.

PHH spermatozoa are less successful than PHL particularly when the two are competing for ova in the same female. The difference may be caused in part by slower penetration by PHH spermatozoa. The smaller number of functional PHH as compared with PHL spermatozoa together with the slower penetration, and perhaps other factors, sometimes lower the fertilizing potency of a PHH ejaculate below the threshold necessary for fertilization of most of the available ova. Frequently none of the ova are fertilized.

I. INTRODUCTION

Parameters for the strains used in this study (Weir, 1962) include a difference in sex ratio (PHH 52.8 ± 1.00; PHL 41.8 ± 0.93) and a difference in litter size. Litters sired by PHL males averaged 0.3 to 1.5 more mice per litter than litters sired by PHH, and this is independent of the strain of female. The strains A/He, AKR, C3H and BALB/c and the outbred "K" stock were used (Weir, 1960, 1962). The sex ratio difference, attributable to the male, is not due to differential mortality in the last trimester (Beck, 1957). Finn (1964), using randomly bred mice, found an effect of the individual male on litter size; Krzanowska (1960) found an effect of strain of male on litter size in the P inbred line.

The present study was undertaken to determine the nature of the physiological difference between PHH and PHL spermatozoa. PHH spermatozoa seem to be functionally deficient.

The effect on litter size that shows up statistically may be due to a number of factors having threshold effects. Litter size may be affected by insufficient numbers of functional spermatozoa at the site of fertilization at the crucial time, by loss of fertilized ova before implantation, or by loss after implantation. The number of spermatozoa at the fertilization site could be limited in several ways. Perhaps the most important of these would be the number of spermatozoa in the ejaculate. The number of motile spermatozoa in an ejaculate required to prevent reduction in fertilization rate in 129/Re, C57BL/6 and F_1 hybrids of these strains is more than 500,000 (Baker 1962). According to Chang (1958) the large number of spermatozoa ejaculated is necessary so there will be enough strong ones to survive in the female tract, especially if ovulation is late. Krzanowska (1964a), in explaining the longer time required for fertilization in inbred mice as compared with outbred, pointed out that the proportion of spermatozoa with full fertilizing capacity is lower in inbred males. Thus the number of spermatozoa ejaculated from an inbred male reaching the fertilization site could be a limiting factor in litter size, particularly in a strain of low fertility.

The number of spermatozoa that reach the fertilization site in the female is limited by the uterotubal junction and probably by the isthmus of the oviduct. Braden and Austin (1954a) found an average of about 17 spermatozoa per tube at the fertilization site in the mouse 10 to 15 hours after copulation. A reduced number of spermatozoa at the fertilization site at the optimal time for fertilization may be related to male mating behavior. Weir (1962) reported copulation by PHH males with females in late estrus, resulting in reduced litter size. PHH males with continuous access to females may also copulate before the optimal time for fertilization. Not only must spermatozoa reach the ampulla of the oviduct, but also there must be an adequate number with unimpaired function. Function might be impaired by a slower than normal capacitation, by inadequate motility, or by reduced ability to penetrate cumulus cells, zona pellucida or vitellus. Necessity of capacitation of mouse spermatozoa has been suggested by Braden and Austin (1954b) and by Krzanowska (1964a). According to Cross (1958) motility is crucial only for penetration of the ovum. Krzanowska (1960, 1961, 1962) found a decrease in number of ova fertilized in inbred compared to outbred and crossbred mice. The greatest reduction in litter size occurred at fertilization and from implantation to the 12th day of pregnancy (Krzanowska 1961). Outbred males improved the fertilization rate in inbred females (both E and P lines). Fertilization rate in outbred females was reduced by P line inbred males (Krzanowska, 1960).

Falconer (1960) and Falconer and Roberts (1960) found reduced fertility of inbred females was due almost entirely to preimplantation loss. Differences in male fertility contributed only 10% or less of the litter size variation, however. McCarthy (1965) found that most of the loss due to inbreeding was early post-implantation loss in CBA/Fa, C57/Fa and R111/Fa mice. He found no male strain effect. Lyon (1959) also found post-implantation mortality due to inbreeding.

The experimental procedures utilized in the study to be reported here included: (1) artificial insemination using combinations of PHH and PHL spermatozoa; (2) counts and classification of ova 21 to 57 hours after copulation and counts of fetuses, corpora lutea and resorptions at 14 to 17 days after copulation to determine preimplantation and post-implantation losses; (3) determination of number, viability and morphology of spermatozoa from the vas deferens and from ejaculates of PHH and PHL, and the proportion of morphologically abnormal spermatozoa in the uterus and in the oviduct.

II. ARTIFICIAL INSEMINATION

The mating of 105 PHL females (treated to induce ovulation) to PHL males with seminal vesicles tied, followed by mating to intact PHH males, resulted in two mixed litters and a total of only 8 litters in all. This, together with results from artificial insemination of PHH and PHL females in induced estrus indicates that females of these strains do not respond well to PMS and HCG nor to PMS and progesterone. Some females did not ovulate, some did not copulate, and some that copulated did not produce litters.

In place of mixed matings, artificial insemination was employed to obtain mixed pools of PHH and PHL spermatozoa. In a mixture spermatozoa from one male may be superior to those from another. Beatty (1960) found differences in success of spermatozoa from two different rabbits when they were mixed and inseminated. Admixture of spermatozoa from more rabbits seemed to increase the percent of inseminations yielding litters. Edwards (1955) demonstrated an apparent superiority of spermatozoa from one strain (C3H) when C3H, REB and G spermatozoa were used in all combinations of two types as well as a mixture of all three types. Southard, Wolfe, and Russell (1965), on the other hand, found that (129/Re x C57BL/6)F_1 spermatozoa from dystrophic males were of about equal potency to those from non-dystrophic F_1 males when the two were mixed and inseminated. Data from Weir (1962) on mixed litters from PHH and PHL double matings showed that this *in vivo* mixing of the spermatozoa accentuated the superiority of PHL spermatozoa. PHL spermatozoa showed a greater superiority in number of progeny produced in the mixed litters than in the single litters. Females were caged continuously with one male of each strain.

MATERIALS AND METHODS

Comparison of sperm extenders. A pilot study was performed to compare the following sperm extenders: Locke's solution with extra glucose (Snell, Hummel and Abelmann, 1944); 9.5% non fat dry milk heated for ten minutes or more and cooled prior to use (Dziuk and Runner, 1960); a 2:1 mixture of 9.5% non fat dry milk and 0.85% saline; 0.65% saline; the yolk citrate, alcohol sugar extender that is used for cattle by the Kansas Artificial Breeding Service Unit; modified Krebs Henseleit Ringer solution (Bhattacharya 1962) without the aureomycin-HC1; egg yolk citrate extender number 3 of Fox and Burdick (1963) decanted from its settled solids and lacking the glycerol; a 1:1 mixture of the egg yolk citrate with modified Krebs Henseleit Ringer solution; and the egg yolk citrate extender with 800 units/cc penicillin and 800 μg/cc streptomycin. In the second experiment the extenders used were 0.85% saline, the egg yolk citrate extender of Fox and Burdick modified as described above, egg yolk citrate that had had CO_2 bubbled through it, and two egg yolk citrate extenders identical to the first one except that the egg yolk was reconstituted dried yolk. Both of these were prepared with Armour Creameries Cloverbloom powdered egg yolk. One was standard type and the other was Type Y, which contains 10 parts corn syrup solids to 90 parts liquid egg yolk. The Type Y yolk was provided by the Kansas Artificial Breeding Service Unit. The pH of all extenders was adjusted to within 0.2 of a pH unit of neutrality. In most cases it was adjusted within 0.1 of a unit. Bishop and Walton (1960a) reported 7.5 as the optimum pH for mammalian spermatozoa and metabolism, although this varies among different mammals and the range of tolerance is quite wide. Contents of vasa deferentia from PHH and PHL males were stripped into 0.10 cc of 0.65% saline in separate depression slides. Two sets of extenders were used, 0.15 cc per tube, one set for each strain. After the spermatozoa were thoroughly mixed in the 0.65% saline, an aliquot of an amount expected to make a dilution appropriate for counting was pipetted into each extender and mixed. An estimate of percent motility was made by haemacytometer examination and checked several hours later. Criteria for judging the extenders were: (1) length of time motility was retained; (2) percent viability as determined by nigrosin-eosin smears. For each haemacytometer count notes were made on type of motility, i.e., speed of motion and whether or not the spermatozoa were making forward progress. In the first series, using nine extenders, the nigrosin-eosin smears were prepared within 8 hours after spermatozoa were placed in the extender. In the second series of five the smears were made within 4 hours after spermatozoa were put in the extenders. Each sperm suspension was mixed with the stain for about 30 seconds prior to spreading. After nigrosin-eosin slides were prepared, all tubes were immersed in water at room temperature and placed in the refrigerator, thus effecting a gradual cooling. In the first series spermatozoa were examined via haemacytometer at two, four, six, and seven days. In the second series they were examined at two and five days. Sperm suspensions were allowed to come slowly to room temperature prior to examination.

INSEMINATION. For artificial inseminations egg yolk citrate extender with glycerol was used in addition to the above. The one selected in the end as most suitable was the 9.5% non fat dried milk with antibiotics and ascorbic acid added. Ascorbic acid concentration ranged from 0.05 mg per ml to 0.39 mg per ml. In most cases the range was 0.20 to 0.34 mg per ml. The procedure for insemination was similar to that of Dziuk and Runner (1960). Most of the females had been induced to ovulate by means of PMS and HCG (2.0 or 2.5 i.u.) given intraperitoneally with an interval of about 37 to 38 hours between injections. For some earlier inseminations some of the females in each group were given 0.5 to 1.0 mg of progesterone, whereas others were given HCG as the second injection. In those groups that had litters 4/8 of the HCG-injected females had litters, while 0/8 of the progesterone-injected females had litters. The progesterone dosage for six of the eight females was 0.5 mg. Females in post partum and cyclical estrus were used for some inseminations. Cyclical estrus was determined by vaginal smears and used only for PHL females which showed weak response to gonadotrophins. After trying also PHH, C3H/He, AL/N, F_1(AL/N x C57L), C57BL/6 and BALB/c, BALB/c females became the strain of choice because of their capacity to respond to gonadotrophins and because eye pigment differences visible at birth allow identification of offspring sired by PHH or PHL males. The vasectomized males, used to provide the vaginal plug, included PHL, PHH, C3H/He and F_1(PHL x PHH). The F_1 males seemed most suitable because (1) regeneration of vasa deferentia would be revealed by 50% of the progeny being phenotypically distinguishable from both PHH and PHL, (2) they copulate quickly and are likely to mate when the female is in the optimum state of receptivity. Regeneration of vasa deferentia occurred in one of the F_1 males. Subsequently, in addition to removal of approximately one half inch from each duct, the end adjoining to the epididymis was tied.

Vasa deferentia were stripped into the extender in a CO_2-enriched atmosphere, PHH and PHL spermatozoa being kept in separate depression slides. In all but the first few inseminations some epididymal spermatozoa were introduced by making one cut through the cauda epididymis and pressing out the contents in the depression slide adjacent to the extender. These contents were then stirred into the extender. After the spermatozoa were carefully mixed with the extender a haemacytometer count was made on a 1:10 dilution from each strain. For some inseminations spermatozoa from the two strains were mixed together prior to insemination. In others PHH spermatozoa were inseminated first followed at varying time intervals by PHL spermatozoa. The time intervals were 8 to 21 minutes, 38 to 67 minutes, and 69 to 78 minutes. Intervals longer than these were tried, but only for a few inseminations. When an equal number of males from the two strains was utilized the number of motile spermatozoa from PHH was noticeably smaller than that from PHL males. Roughly equivalent numbers could usually be obtained by using twice as many PHH males as PHL. To increase the percentage of motile PHH spermatozoa as well as to obtain spermatozoa that were already capacitated, or at least partially so, PHH ejaculates that had been in the uterus for up to two hours were used to supplement the source from vasa deferentia. To inseminate a group of three females spermatozoa were used from four PHL males, six PHH males, and as many PHH ejaculates as could be obtained from six fertile males each given a hormonally primed female. Some females were inseminated with only PHH spermatozoa. In several groups of females one or more of the females were given only PHH spermatozoa while the other females in the group were subsequently given PHL in addition to the PHH spermatozoa. In one such group the delayed supply of PHL spermatozoa was provided by copulation with intact PHL males. Similar experiments were performed with PHL spermatozoa. That is, some females were given only PHL spermatozoa and some were given PHL followed by PHH. Spermatozoa were inseminated by means of a blunted 22 gauge needle 11 to 14 1/6 hours after HCG injection. Most inseminations were between 12½ and 14 hours after the HCG.

In a number of inseminations, hyaluronidase,* ß-amylase,* fructose, bicarbonate, or an extract of PHL spermatozoa was added to the PHH spermatozoa. Concentrations of hyaluronidase chosen for this work were 1, 2, and 4 mg per ml. At 2 mg, and especially at 4 mg per ml, there may have been a deleterious effect on the spermatozoa as judged by examination in the haemacytometer. More than the usual number seemed to be bent double. Dosage of ß-amylase was selected on the basis of work on rabbit sperm by Kirton and Hafs (1965), who used 0.1 or 1.0 mg per 100 ml of the extender. Concentrations chosen were 0.3, 0.8, and 3.6 mg per ml. Concentrations of fructose ranged from 2.5 to 3.0 mg per ml. The extract of PHL spermatozoa was prepared by means of a tissue homogenizer or by alternate freezing and thawing. Spermatozoa from vasa deferentia and epididymis of 4 to 6 PHL males were stripped into the usual milk extender. After the cells were broken by one of the afore-mentioned procedures, cells and cellular debris were removed by centrifugation and part of the supernatant was used as the extender for the PHH spermatozoa. In all the inseminations in which an extra ingredient was added to the extender for the PHH spermatozoa, PHH spermatozoa were inseminated before PHL. The time interval between inseminations ranged from 46 to 83 minutes.

RESULTS

Comparison of sperm extenders. There was a tendency toward higher viability in the milk and milk saline extenders, but more active motility in most of the others, including the egg yolk citrate extenders. The milk, milk saline, and egg yolk citrate extenders provided longest duration of motility. Penicillin and streptomycin added to the egg yolk citrate extender did not affect viability or type of motility and seemed to prolong duration of motility. The yolk citrate alcohol sugar extender, which is of proven value for bull spermatozoa, was noticeably inferior to the other extenders. Most of the motility had been lost one or two hours before the nigrosin-eosin slides were prepared. The remaining motile spermatozoa were moving very slowly, so nigrosin-eosin slides were not made.

Insemination. The sex ratios derived from inseminations, 71/202=0.351±0.035 for PHL and 19/37=0.514±0.082 for PHH, are strikingly similar to the strain parameters. Comparison of PHL litters of 3 or fewer (9/29=0.310±0.093) with litters of 4 or more (49/144=0.340±0.042) reveals no difference in sex ratio. Results from hyaluronidase-treated inseminations are not included in these values. The number of progeny from litters of three or fewer is admittedly small. If X-bearing spermatozoa have an advantage, for example, greater ability to penetrate, the excess of XX zygotes might be accentuated when there are not enough spermatozoa to fertilize all of the ova. The only agent that seemed to exert an affect on sex ratio was hyaluronidase. Since it was added to PHH spermatozoa only, it would have to remain in the uterus in large enough quantities to affect the PHL spermatozoa inseminated 46 to 83 minutes later. Sex ratio from PHL spermatozoa under these conditions was $12/23=0.522\pm0.104$, and for inseminations without hyaluronidase it was $52/156=0.335\pm0.040$ ($X^2_1=3.10$, $0.05<P<0.10$). For PHH spermatozoa the ratios were $5/6=0.833$ with hyaluronidase, and $14/29=0.483\pm0.093$ without it ($X^2_1=2.46$, $0.10<P<0.20$).

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The effectiveness of the PHH spermatozoa in the inseminations was poor. Even when many more motile PHH than PHL spermatozoa were inseminated there were more progeny from PHL than from PHH spermatozoa. From these inseminations the percent of progeny from PHH spermatozoa constituted $5/31=16.1$ percent of the total. With one exception, a case of insemination with spermatozoa from PHH only, there were no full size litters from PHH spermatozoa. The average number of live progeny from BALB/c females induced to ovulate with gonadotrophins and mated to fertile males was $42/7=6.0\pm1.05$. The mean number of ova from BALB/c induced to ovulate with gonadotrophins was found by H. Glenn Wolfe (unpublished data) to be $204/20=10.2\pm1.32$. The number of progeny from inseminated PHH spermatozoa varied from one to two in inseminations in which both strains of spermatozoa were used and from one to 14 (with 10 live) in cases in which only PHH spermatozoa were inseminated. Excluding the one large litter, the numbers varied from one to four (three live). Number of progeny per litter from PHH and PHL spermatozoa are shown in Table 1. Litter sizes from all double inseminations of BALB/c females, exclusive of those on females in post partum estrus, were $30/22=1.4$ for PHH spermatozoa and $165/33=5.0$ for PHL spermatozoa. Not only were litters from PHH spermatozoa small, but also they occurred in only a small fraction of the females inseminated. Results are shown in Table 2. From Table 1 a comparison can be made between the fraction of females that had progeny when one strain of spermatozoa was injected and the fraction that had progeny when both strains of spermatozoa were injected. The fraction that had litters when given gonadotrophins and mated to known fertile males was 7/10. Southard, Wolfe and Russell (1965), using hormonally primed (129/Re x C57BL/6)F_1 females, found the fraction to be $127/317=43\%$ from natural matings. There were three groups of inseminated females in which litters occurred both in the subgroup given only PHH spermatozoa

TABLE 1. Litters from BALB/c females artificially inseminated with PHH, PHL, or combinations of PHH and PHL spermatozoa.*

	Single inseminations		Double inseminations					
			Single		Mixed		Totals from	
	PHH sperm	PHL sperm	PHH sperm	PHL sperm	PHH sperm	PHL sperm	Mixed	PHL sperm
Litters/♀♀ inseminated	5/24	3/8	0/90	13/90	— 9/90 —		9/90	22/90
Number of mice born	25	12	....	60	10	55	65	115
Mice per litter	5.0	4.0	....	4.6	1.1	6.1	7.2	5.2
Range of litter size	1-10	1-8	....	1-10	1-2	2-9	3-10	....

* Only live progeny were counted.

Inseminations using hyaluronidase and those with time interval between inseminations exceeding 67 minutes are not included in the results from double inseminations.

and in the subgroup given spermatozoa from both strains. In these inseminations PHH spermatozoa from a single source in approximately equal numbers were inseminated into the females given only PHH spermatozoa, as were inseminated into the females given both strains of spermatozoa. Results were: three of the four females receiving only PHH spermatozoa had litters; mean litter size was 2.7 with a range of 1 to 4. Three of the five females receiving spermatozoa from both strains had litters, but only one of these had progeny from PHH spermatozoa. This litter had one mouse from PHH spermatozoa. The work of Weir (1962) showing an enhanced superiority of PHL over PHH spermatozoa in mixed litters is supported. The present data are not statistically significant, but consistent. There were more progeny per litter from PHH spermatozoa and a larger proportion of inseminated females having progeny from PHH spermatozoa in single than in double inseminations. If the inferiority of PHH to PHL spermatozoa is in fact accentuated when both strains of spermatozoa are inseminated, the difference between the strains could be expressed between ejaculation and fertilization, or it could result from greater loss of ova fertilized by PHH spermatozoa in mixed litters than in litters from PHH spermatozoa alone. It might be argued that much of this loss occurs after implantation due to crowding in mixed litters. Table 3 shows post-implantation losses obtained by comparing litter size with number of implantation scars. Unfortunately, counting of implantation scars was confined to the latter part of the investigation. The data indicate that loss of zygotes from PHH spermatozoa is no greater than loss from PHL spermatozoa. Also, the presence of zygotes from PHH spermatozoa in litters from double inseminations does not seem to increase post-implantation loss appreciably. Greater loss from crowding might be expected in the mixed litters since litter sizes tended to be higher. There is

TABLE 2. Litters from artificial insemination of BALB/c females with spermatozoa from PHH and PHL males.*

	PHH spermatozoa not precapacitated		PHH spermatozoa precapacitated				
				PHH sperm inseminated first			
	Mixed insemination	PHH sperm inseminated first. 8-21 min. interval	Mixed insemination	8-21 min. interval	38-67 min. interval	69-78 min. interval	TOTAL
Litters/♀♀ inseminated	1/14	2/8	2/16	1/4	12/31	7/16**	25/89
Litters with mice from PHH sperm/♀♀ inseminated	1/14	2/8	1/16	1/4	3/31	6/16	14/89
Live progeny from PHH sperm/total live progeny	1/3	2/12	2/12	1/8	3/67	9/33	18/135

* Data shown for the 38-67 minute interval and the 69-78 minute interval were obtained using the same extender (9.5% milk with antibiotics and ascorbic acid added). Results from inseminations utilizing hyaluronidase are not included.

** Includes one litter consisting of progeny from PHH spermatozoa only. In every other case tabulated litters having progeny from PHH also had progeny from PHL spermatozoa.

no compelling reason to believe that the slightly higher post-implantation loss in mixed litters, compared to litters from single inseminations, was due to differential loss of embryos. Alternative explanations for low effectiveness of PHH spermatozoa include later arrival of PHH spermatozoa at the surface of the zona pellucida or a slower maturation of PHH than PHL spermatozoa. However, comparison of litters from inseminations with PHH spermatozoa that were precapacitated (spent some time in a uterus prior to insemination) with those from PHH spermatozoa not so treated showed no effect from precapacitation (see Table 2). Insemination of PHH spermatozoa 38 to 67 minutes before injection of PHL spermatozoa actually seemed to reduce the effectiveness of PHH spermatozoa. Possible explanations are: (1) If PHH spermatozoa were more effective in mixed inseminations than with the 38-67 minute head start, the difference might be attributed partly to a difference in extenders. Not many of the mixed inseminations were done with ascorbic acid in the milk. Ascorbic acid may cause a higher percentage of conception from PHL spermatozoa. Either it does not help PHH spermatozoa or its influence was offset by a seasonal effect. (2) At the longer intervals the PHH spermatozoa did not have the benefit of the copulation and plug nearly as soon after insemination as did the PHL spermatozoa. Copulation stimulates uterine contraction and probably speeds transport of spermatozoa, as demonstrated for the cow by Van Demark and Hays (1952). Spermatozoa

TABLE 3. Loss of implanted fetuses as determined by counts of implantation scars.

	Double inseminations (both kinds of sperm)			Single inseminations	
	Litters containing progeny from: both strains	PHH sperm only	PHL sperm only	PHH sperm	PHL sperm
Mean number last	2.9	0	2.5	1.3	1.7
Range	1-6	–	0-6	0-5	1-2
n	9	2	8	4	3*
Mean litter size (live + dead)	6.1	1.0	4.5	5.0	6.5
Dead at birth	0.1	0	0.1	1.7	2.0
Range of litter size	2-10	–	2-7	1-14	5-8

* One female was noted pregnant but the litter was never found. She had one implantation scar. Mean litter size, number dead at birth, and range of litter size are based on 2 rather than 3 individuals.

from the later insemination (PHL) are likely to be carried into the oviduct soon after insemination. Also, the plug prevents loss of inseminated sperm suspension due to seepage through the cervix. (3) For both mixed inseminations and those in which the interval between injection of PHH and PHL spermatozoa was 21 minutes or less, the PHL spermatozoa were held *in vitro* for a longer time prior to insemination. For these inseminations the vasa deferentia from the two strains were stripped alternately, whereas with longer intervals PHL males were not opened until after PHH spermatozoa had been inseminated. (4) If the ova were not released until some time after PHH insemination, the interval between inseminations would merely allow more time for PHH than PHL spermatozoa to deteriorate. The interval would be a handicap to PHH spermatozoa rather than a help.

When β-amylase was included in the extender used for PHH spermatozoa no improvement in performance of PHH spermatozoa was evident. The time interval between insemination of PHH and PHL spermatozoa ranged from 54 to 64 minutes. Of a total of nine females inseminated two had litters. One of these consisted of only one mouse which was dead at birth. Paternity was unknown since this cannot be determined accurately in stillborn mice. None of the females had any known (live) progeny from PHH spermatozoa. Although numbers of motile spermatozoa in counts from PHH were low, progeny were produced in other inseminations with estimates of number of motile PHH spermatozoa as low or lower. ß-amylase has been shown to be the capacitating factor for rabbit spermatozoa (Kirton and Hafs, 1965), so may perform a similar function in mice.

Results from precapacitation of PHH spermatozoa, from giving a head-start of up to 67 minutes and from including ß-amylase in the suspension, argue against the hypothesis that the superiority of PHL over PHH spermatozoa in double inseminations is caused by more rapid capacitation of PHL spermatozoa.

When the interval between inseminations was increased to 69-78 minutes, PHH spermatozoa were more successful than when the interval was shorter (see Table 2). A comparison of the 69-78 and 38-67 minute intervals gives $X^2=10.88$ ($P<0.001$); comparing the 69-78 and 0-67 minute intervals, $X^2=8.26$ ($P<0.01$). Of the mixed inseminations and those with an 8-21 minute interval few were done with the milk (with antibiotics and ascorbic acid) extender. Only the inseminations utilizing this extender were included in the comparison. The difference is not significant when the 69-78 minute interval is compared with the 8-21 minute interval and mixed inseminations, but the reasons given previously for poor performance of PHH in the 38-67 minute interval relative to shorter intervals and mixed inseminations are applicable here also.

Hyaluronidase added to the portion of the extender used for PHH spermatozoa seemed to increase the number of successes of PHH relative to PHL spermatozoa. The time interval between inseminations, 46-62 minutes, was comparable to that of the 38-67 minute interval group. Results from those inseminations in this group in which neither hyaluronidase nor the PHL sperm extract were used are included for comparison in Table 4. Results from inseminations that utilized hyaluronidase were compared with those from all other double inseminations, from zero through a 67 minute interval. Only results from inseminations in which the extender consisted of skim milk with antibiotics and ascorbic acid were included ($X^2=3.65$, $0.05<P<0.10$).

Results from inseminating an extract of PHL spermatozoa along with PHH spermatozoa are shown in Table 4. The effect, if any, was small.

Fructose was used in the extender for insemination of 10 females. With one of the groups, a group of three females, the fructose was included only in the extender used for PHH spermatozoa. In the remaining groups it was used for both strains of spermatozoa. Time interval between inseminations ranged from 44 to 96 minutes. Three of the 10 inseminated females had litters. The progeny were: one from PHH spermatozoa, 5 from PHL. There was no detectable enhancement of sperm motility except in one insemination, and no litter was produced from it. Nevo (1965) found that for bull, ram, and cock spermatozoa the respiratory rate and critical oxygen concentrations were not appreciably altered by the presence of glucose or fructose. Although additional testing might have shown a beneficial effect on PHH spermatozoa, the effect of fructose was not striking.

Table 4. Effect of hyaluronidase and extract of PHL spermatozoa on function of PHH spermatozoa in double inseminations.*

	Time intervals between PHH and PHL inseminations in minutes	Litters/♀♀ inseminated	Litters with mice from PHH sperm/♀♀ inseminated	Live progeny from PHH sperm/total live progeny
Hyaluronidase with PHH spermatozoa	46-62	6/13	4/13	5/24
Extract of PHL spermatozoa inseminated with PHH spermatozoa	59-69	5/9	2/9	2/24
Neither extract nor hyaluronidase	38-67	9/25	2/25	2/47

	With hyaluronidase	Without hyaluronidase	
PHH progeny	5	2	7
PHL progeny	19	45	64
	24	47	71

$X^2 = 4.91$

$0.02 < P < 0.05$

* The extender consisted of skim milk with antibiotics and ascorbic acid.

Hamner and Williams (1964) reported stimulation of respiration in rabbit, rooster, bull and human spermatozoa by bicarbonate. The concentration for maximal stimulation in rabbit spermatozoa was 2.36×10^{-3}M. Bicarbonate was placed in the extender used for the PHH spermatozoa in the insemination of one group of females. The concentration used was 2.2×10^{-3}M. No litters were produced, but in three other groups of females bicarbonate was contained in the extender used for both PHH and PHL spermatozoa. Three of the nine females had litters with one mouse from PHH spermatozoa, 13 from PHL. The numbers were small, but no improvement in success of PHH spermatozoa was observed. Stimulation of respiration prior to insemination would be harmful if early expenditure of energy shortens the period of motility. Examination of small samples of sperm suspensions set aside before insemination with the remainder has confirmed that PHH spermatozoa are likely to lose motility more quickly than PHL.

Since haemacytometer examination of spermatozoa showed that a consistently higher proportion of viable PHH than viable PHL spermatozoa were bent double, a comparison was made of ejaculates from PHH and PHL males. Two nigrosin-eosin slides were made per ejaculate and two counts were made per slide. Four ejaculates from 3 PHH males had a mean of 24% of all spermatozoa viable and bent double behind the midpiece. The range of counts was 12% to 34%. A mean of 2% of all spermatozoa were viable and bent at the neck. The range of counts was zero to 5%. Three ejaculates from 2 PHL males had a mean of 5% of all spermatozoa that were viable and bent double behind the midpiece. The counts ranged from zero to 11%. A mean of 6% of all spermatozoa were viable and bent at the neck. The counts ranged from 2 to 13%.

DISCUSSION

Some steps between insemination and fertilization at which PHH spermatozoa might be retarded could be summarized as follows: Capacitation of spermatozoa is believed to be a prerequisite for fertility. Also, spermatozoa must penetrate the cumulus cells, the zona pellucida and the vitellus of the ovum; penetration of the cumulus cells depends upon hyaluronidase carried by the spermatozoa (Austin 1961a). Penetration of the zona pellucida seems to depend upon another enzyme carried by the spermatozoa, called "zona lysin" by Austin and Bishop (1958). Sperm motility is required for at least part of the penetration process. Penetration of the vitellus may or may not depend upon motility. Blandau and Odor (1952) observed that motility was involved in penetration of the vitellus by rat spermatozoa. Austin and Braden (1956) described a more passive penetration by rodent spermatozoa. The vitellus absorbed the spermatozoa.

Most of these factors operating prior to fertilization have been studied by various modifications in the procedure for artificial insemination. The principal reason for testing different extenders was to find one in which the PHH spermatozoa would remain motile in large numbers for a reasonably long period of time. Fructose was also tested for this purpose. Apparently the only way to be sure of having enough functional PHH spermatozoa is to inseminate them in much larger numbers. The required number may not often have been attained. A factor that further decreases the number of functional PHH spermatozoa is the bent condition shown by many of them. Bishop and Walton (1960b) termed the bent tail condition (called looped tail) a secondary abnormality. They stated that secondary abnormalities consist of spermatozoa that appear to have been normally differentiated but subsequently deformed while passing through the male reproductive tract. Decapitate spermatozoa are also included in this category. PHH males with large numbers of decapitate spermatozoa are occasionally found. This condition rarely occurs in PHL males.

Capacitation does not explain the inferior performance of PHH spermatozoa. PHH spermatozoa, given an opportunity to be capacitated prior to insemination and then inseminated up to 67 minutes before PHL spermatozoa, showed no improvement in performance. Braden and Austin (1954b) suggest capacitation time to be an hour or more in the mouse.

Data from inseminations with hyaluronidase added must be interpreted with caution. The effect of hyaluronidase needs to be tested by dividing equally a dense suspension of spermatozoa between extender with and extender without hyaluronidase. Chang (1950) has stated that the hyaluronidase in the spermatozoa is adequate for penetration of cumulus cells and that a supplementary supply is not required. Leonard, Perlman and Kurzrok (1947) found that hyaluronidase introduced into the rat uterus did not get into the oviducts, at least not in large enough amounts to denude the ova. However, spermatozoa might absorb some hyaluronidase from the extender. Emmens and Swyer (1948) showed that rabbit spermatozoa reabsorbed a significant amount of homologous hyaluronidase but not of heterologous (bull) hyaluronidase. If mouse spermatozoa can absorb heterologous (bull) hyaluronidase or if some could enter the oviduct, supplementary hyaluronidase could facilitate penetration of cumulus cells by the PHH spermatozoa. Penetration of cumulus cells in the mouse requires enough time to have caused the extra delay between ovulation and fertilization in the inbred strain with the greater density of cumulus cells (Braden 1958a, 1962). Thus a difference in time required to penetrate the cumulus cells could be partly responsible for the inferior performance of PHH spermatozoa.

An extract from PHL spermatozoa was added to PHH spermatozoa to provide zona lysin as well as any unknown factors. Hyaluronidase would also be provided by the extract. Failure to produce a striking improvement might be because the needed factors were not provided by the extract or because concentrations carried into the oviduct were inadequate. Higher concentrations should be tested. In the race with PHL spermatozoa, once a spermatozoan penetrates the zona and attaches to the vitellus, the block against polyspermy and the zona reaction are elicited and the race is over (Austin and Braden, 1956; Austin, 1959; Braden, Austin and David, 1954). Hence poor competition of PHH with PHL spermatozoa can not be caused by deficiency of a factor required for penetration of the vitellus.

Interpretation of the data requires information on timing. If mature ova are not available until after the PHL spermatozoa are inseminated, putting PHH spermatozoa in first would be a handicap rather than an aid, allowing more time for deterioration without providing an effective headstart. Lin and Bailey (1965), from an investigation not intended to establish exact time of ovulation of BALB/c females, found that ovulation was completed by 14 hours after the HCG injection. Ovulation could conceivably have been completed earlier. Marston and Chang (1964) determined time of ovulation in Swiss Webster mice. They found that mature females had completed ovulation within 12 hours after HCG injection. Some females had ovulated by the tenth hour. Immature females required 14 hours to complete ovulation. Gates and Beatty (1954) reported that ovulation in immature hybrid mice occurred 11 to 13 hours after HCG injection. A preliminary study of induced ovulation in BALB/c females has shown that ovulation has begun in some females at 12 hours, but apparently not at 11 hours after HCG injection. There were ova present at 11 hours, but they were denuded and most likely were released somewhat earlier as a result of the PMS alone. Since they were denuded, most of them were probably too old for normal fertilization and development. Marston and Change (1964) showed that ova from mature Swiss Webster mice were largely denuded (represented by 0.2 on a scale of 0 to 6) by 30-31 hours after HCG, which would be some 18 hours after ovulation. At this time there was a sharp drop in number of ova penetrated. Lewis and Wright (1935) reported ova denuded as early as 12 hours after copulation.

Usually the PHH spermatozoa were inseminated more than 12 hours after the HCG injection so that in many cases ova should already be present in the oviducts. If maturation of ova membranes is necessary, this would have a chance to occur while the spermatozoa are maturing and being transported to the fertilization site. Data from Braden and Austin (1954b) indicated that 1½ to 2 hours might be required for egg maturation, but Edwards and Gates (1959) reported that little time was needed for maturation of egg membranes. According to Edwards and Gates, approximately 70 minutes elapsed between ovulation and penetration. The 70 minute interval would include the time required for penetration of the cumulus cells and the zona. Transport of mouse spermatozoa to the site of fertilization requires ¼ to 1¼ hours (Merton, 1939; Lewis and Wright, 1935; Braden and Austin, 1954b; Braden, 1962). Fifteen minutes represents the minimum. Braden and Austin (1954b) suggest ¾ hour as the mean time required. Yanagimachi (1963) has reported more rapid sperm transport after ovulation than before ovulation in the hamster. This may be true in the mouse, also. Since in artificial insemination the stimulus provided by the plug is delayed, uterine contractions are unlikely to occur at the time the spermatozoa are injected. However, injection of spermatozoa deep into the uterus may have a compensatory effect on the time of transport.

CONCLUSIONS

PHH spermatozoa are inferior to PHL spermatozoa in ability to fertilize ova. The reasons remain obscure, but the following indicate that PHH spermatozoa penetrate more slowly than do PHL spermatozoa: (1) A possible accentuation of PHL superiority when both strains of spermatozoa are inseminated as compared with single inseminations. (2) Improvement of PHH performance when the interval between PHH and PHL insemination is increased to 69 minutes or more. (3) A possible beneficial effect of hyaluronidase upon performance of PHH spermatozoa.

The poor conception rate from PHH spermatozoa may be from failure of enough of them to maintain vigorous motility for a long enough period of time.

III. PREIMPLANTATION AND POST-IMPLANTATION LOSSES

Design of the experiment involving ova counts was similar to that of Whitten and Dagg (1961). In addition to differences in counts and developmental rates differences with respect to time of copulation during the diurnal cycle could be detected. F_1(PHL ♀ x PHH ♂) and F_1(PHH ♀ x PHL ♂) were used in addition to the two strains of inbred males. Since pH is correlated with lactic acid levels, and lactic acid levels are inherited in a manner that suggests sex linkage (Weir 1962), the F_1 males were used to test for possible sex-linked inheritance of the litter size effect.

MATERIALS AND METHODS

Single pair matings were made, PHH, PHL, and C3H/He females with PHH and PHL males, and PHH and PHL females with F_1(PHL ♀ x PHH ♂) and F_1(PHH ♀ x PHL ♂) males. The light cycle was adjusted to 19 hours of light and 5 hours of darkness with lights coming on at 3:00 p.m. and going off at 10:00 a.m. Females were introduced within the two hour interval preceding the dark phase. With few exceptions the females were 70 to 120 day old virgins that had been stored up to seven per cage. The females were examined for vaginal plugs at 8:00 a.m., 3:00 p.m., and at approximately 10:00 p.m. Ova were examined at intervals ranging from about 21 to 57 hours after the estimated time of copulation for all four types of pairings involving PHH and PHL males and females (two *inter se* and two crossed). The time of mating was considered to be the midpoint of the dark period if the plug was found at 3:00 p.m. (at the end of the dark period). Otherwise, mating was considered to have occurred half way between the time the plug was detected and the previous time the female was examined for the presence of a plug. If the vulva was recorded as red or moist from frequent intromissions by the male, and a plug was observed at the subsequent examination, copulation was considered to have occurred within one hour. Ova from C3H/He females were examined 36 to 54 hours after the estimated time of copulation. Females paired with F_1 males were examined for ova 27 to 57 hours after estimated time of copulation; most were examined 37 to 53 hours after copulation. The *inter se* pairings and reciprocal crosses of PHH and PHL males and females were checked for loss of ova at the longer intervals. Mean number ovulated from each strain of female examined up to 32½ hours was compared with mean number from females examined 40 to 57½ hours after copulation. There was no detectable loss at the longer time intervals. The ova were obtained by flushing approximately 0.02 cc of Ringers solution through the oviduct. The cut for removal of the oviduct was made near the ovarian end of the uterine horn. The oviduct with accompanying ovary was transferred to a depression slide containing Ringers solution where the ovary, fat and mesentry were detached by means of micro dissecting forceps. After the oviduct was blotted and transferred to clean Ringers solution, the ovarian end was freed. Following a second blotting and transfer, the end was slipped over a blunted 31 or 33 gauge needle and the contents flushed out. A gentle rotary motion of the depression slide facilitated settling of ova in the center of the slide. Corpora lutea were counted under a dissecting microscope at 10 or 19.5 magnification. Ovaries were measured to the nearest ½ millimeter and in some cases weighed. Ova were examined at 19.5 X and classified as normal fertilized or as one of several abnormal types. Normal cleavage was used as the criterion for fertilization of ova when 27 hours or more had elapsed since estimated time of copulation. In many cases normally cleaved zygotes were found at the shorter intervals, such as 23 hours. If none were cleaved, the ova were not classified unless they were all abnormal or unless two polar bodies could be clearly seen on the normal one-celled ova. Occasionally a higher magnification, 60 X, was used. Zygotes with too many cells to be counted accurately were transferred to a microscope slide, stained, and examined at 100 X.

Corpora lutea, fetuses, and resorption sites were counted at 14 to 17 days gestation. In most cases the examination was made 15 to 16 days after formation of the plug. Biggers, Curnow, Finn and McLaren (1963) found that corpora lutea begin to regress at about the 17th day.

C3H/He females were paired with PHL and PHH males, one per male, and examined daily until plugs were found. Corpora lutea were examined at 19.5 X magnification.

RESULTS

MALE EFFECTS ON NUMBER OF NORMAL ZYGOTES Results from ova counts are shown in Table 5. There was a consistent but nonsignificant difference in number of normal zygotes attributable to the two inbred strains of males, PHH and PHL. No such difference was detected from the two types of F_1 males. The difference can be partly accounted for by the difference in number of fragmented ova. The difference in number of fragmented ova was largely attributable to a few PHH males. Females with which they copulated had a large proportion of fragmented ova and hence few normal zygotes. When all normal zygote counts of 3 or fewer are omitted, the difference between mean numbers of normal zygotes attributable to the strain of male is reduced from 1.5 to 0.8 for PHH females, from 1.0 to 0.7 for PHL females, and from 1.3 to 0.6 for C3H/He females. There were fewer small zygote counts fol-

Table 5. Classification of ova from *inter se* matings and crosses.

Matings		Mean ova counts per litter						
Kind ♀ ♂	Number	Normal fertilized	Fragmented	Degenerate	Abnormal* zona pellucida	Normal unfertilized	Immature	TOTAL
PHH X PHH	22	9.2±0.79	1.2	0.1	1.2	0.3	0.1	12.1±0.45
PHH X PHL	25	10.7±0.57	0.1	0.5	0.9	0.1	0.04	12.3±0.40
PHL X PHH	24	9.5±0.61	0.6	0.3	0.5	0.3	0.2	11.4±0.37
PHL X PHL	24	10.5±0.49	0.2	0.2	0.4	0.1	0.1	11.5±0.31
C3H/He X PHH	18	8.1±0.60	0.7	0.5	0.3	0.3	0.1	9.9±0.27
C3H/He X PHL	16	9.4±0.37	0	0.4	0.3	0.1	0	10.2±0.29
PHH X F_1(HxL)	10	11.4±0.43	0	0.2	0.5	0	0.2	12.3±0.45
PHH X F_1(LxH)	8	11.3±0.45	0.1	0.9	0.1	0	0.2	12.6±0.50
PHL X F_1(HxL)	12	10.6±0.26	0	0.7	0.2	0	0	11.5±0.40
PHL X F_1(LxH)	11	10.6±0.45	0.2	0.3	0.2	0	0	11.3±0.54

* Empty zona pellucida, zygote with one or more cells outside zona pellucida, or ovum or zygote lacking zona pellucida.

lowing copulation with PHL compared to PHH males. The counts were not included unless there was at least one normal zygote. This precaution was necessary since the purpose of the study was to attempt to isolate causes of smaller litter size coming from PHH sires. If no ova were fertilized obviously there would be no litter. It was found that fragmented ova occurred following copulation with a larger proportion of PHH than of PHL males. The proportion of PHH males was 23/36 and of PHL males 7/29. With 10 of the PHH males fragmented ova occurred following more than one copulation. Several (six) of those for which only one litter containing fragmented ova was recorded were checked only the one time. Fragmented ova occurred following more than one copulation with only one of the PHL males. Two of the other six were checked only once, so there was no opportunity for more than one group of ova containing fragmented ones.

Possible causes of fragmentation include late fertilization (Austin, 1961b; Marston and Chang, 1964) and aging of unfertilized ova (Marston and Chang, 1964). PHH males are not likely to wait until ova have aged before copulating even though they will mate with females in late estrus (Weir, 1962). Probably most or all of the fragmented ova were aged unfertilized ova. Spermatozoa counts were made on ejaculates from 6 PHH males that seemed to be responsible for fragmented ova in females with which they copulated. Two of the males, from which one ejaculate each was examined, transferred no spermatozoa to the female. A third male had a low sperm count (675,000). All three of these males were fertile enough to sire litters although one was kept with a hybrid female for several months and should have sired more than one litter if fertility had been normal. The incidence of litter sizes of 4 or less was rather high among these males (4 of 14 litters). The data show that there can be a sharp fluctuation in spermatozoa counts (from none to enough to sire a litter). Also, failure to fertilize all the ova may not be caused by low spermatozoa counts alone. Two males had spermatozoa counts in the upper end of the range for PHH males. (The highest count that has been found was 11,700,000.)

If the occasional litter with several unfertilized (including fragmented) ova and few normal fertilized zygotes is in part or largely responsible for small litters from PHH males, one would expect to find much of the difference caused by a few small litters. Examination of Weir's data (1960, 1962) shows this to be the case. Omitting litters of 3 or fewer reduces the difference in litter size attributable to the strain of male from 0.6 to 0.2 for K females, and from 1.7 to 1.2 for C3H females. Ten of 145 litters from K females and PHH males had 3 or fewer mice while only one of 102 litters from K females and PHL males had 3 or fewer mice.

According to Beck (1957) more PHH than PHL progeny are lost in the last trimester and at parturition, but these were from *inter se* matings, so maternal effects cannot be separated from effects acting through the zygotes.

ADDITIONAL STRAIN COMPARISONS. There was no detectable difference due to strain of male in developmental rates in any of the combinations (PHH ♀ x PHH ♂, PHH ♀ x PHL ♂, PHL ♀ x PHH ♂, PHL ♀ x PHL ♂, C3H/He ♀ x PHH ♂, C3H/He ♀ x PHL ♂).

There seems to be a consistent tendency for PHH females, compared to PHL and C3H/He, to release more ova (see Table 5), but the difference is small. Also, PHH females compared to PHL tend to have more ova that are broken out of the zona pellucida, but the difference is not statistically significant.

Examination of the corpora lutea showed that there were many cases in which corpora lutea were not distinct enough to determine the number of ova released. Even when they were clearly distinguishable there was not always a one-to-one relationship with ova count. Although corpora lutea were often indistinct in females examined 29 to 57 hours after estimated time of mating, they were even less often distinct at shorter time intervals. Considering only the counts taken during the 29 to 57 hour interval, of the 71 counts where ova were more numerous than corpora lutea 49 differed by only one. Of the 27 cases in which the number of corpora lutea exceeded the number of ova, 19 differed by only one. Of the 61 counts showing an equal number of ova and corpora lutea 11 cases seemed to indicate transmigration of blastocysts from one uterine horn to the other. McLaren and Michie

(1954) have presented some evidence for crossing of blastocysts from one side to the other.

Possible causes for discrepancy between counts of corpora lutea and of ova include failure to distinguish partially confluent adjacent ones (Falconer and Roberts, 1960), delayed luteinization, and, rarely, polyovular follicles (Engle, 1927). Also, there may be a loss of ova (particularly at the longer time intervals) or follicles that have no ovum. Packs of cumulus cells without ova were quite frequently seen, especially when counts were made shortly after copulation. Since comparison of ova counts up to 32½ hours after copulation with those 40 to 57½ hours after gave no indication of loss of ova at the longer intervals, losses were small if they occurred.

A difference between PHH and PHL females with respect to the portion of the light cycle during which they will copulate has been observed. Although the X^2 test for independence does not show statistical significance using light versus dark, inclusion of females that copulated shortly after the start of the light period with those that copulated during the dark gives a significant difference ($X^2_1=10.51$, $P<0.01$). PHH females had a greater tendency than PHL to copulate during and shortly after the dark period. Females having a wet and red vulva at the end of the dark period (3:00 p.m.) and a plug when examined at 10:00 p.m. were assumed to have copulated shortly after the dark period ended. If only the first series of males (seven from each strain) is considered, a significant difference at the 5% level is observed in time of mating of males of the two strains ($X^2_1=4.42$). For the entire group of males, however, the difference is not significant. The greater tendency shown by PHH males to copulate during the dark may be due to their more aggressive mating behavior. They may copulate with those females that are still somewhat refractory during the dark period, whereas PHL males may delay until these females are in optimum estrus.

The elapsed time preceding copulation was shorter and more regular with PHH than with PHL females. A X^2 test for independence shows statistical significance when the number of copulations occurring through the fourth day is compared with those occurring five or more days after pairing ($X^2_1=5.33$, $P<0.05$). The difference between strains is even greater if account is taken of the number of females not copulating when paired with males for a period of time in excess of six days ($X^2_1=9.97$, $P<0.01$). The longest time required for a plug was 12 days for PHL females and eight days for PHH. C3H/He females were not observed concurrently with the other two strains, but the data available show they copulate sooner after pairing than do PHL females ($X^2_1=5.07$, $P<0.05$).

Fetal counts. Results from fetal counts are shown in Table 6. Corpora lutea were larger, and in most cases more distinct than at preimplantation stages. All but one of 17 resorptions from PHH males and all but one of

TABLE 6. Fetuses and corpora lutea from C3H/He females mated to PHH and PHL males.

	Number of litters	Corpora lutea (mean)	Fetuses (mean)	Resorptions (mean)	Preimplantation loss
PHH males	21	9.8±0.35	7.6±0.42	0.8	1.4
PHL males	20	9.4±0.34	8.2±0.36	0.4	0.8

9 from PHL males were very early post-implantation losses—prior to formation of the placenta. In one litter from a PHH sire the preimplantation loss was 7 out of 10. When this litter is omitted, the mean preimplantation loss from PHH sires was 1.1. All of the eleven PHH males used were known to be fertile. The several that did not sire litters or fertilize ova were not used. Several of the PHL males were not tested in advance for fertility, but only one of 20 females mated to PHL males failed to conceive from the first copulation. Eight of 22 females with PHH males failed to conceive from the first copulation. In two cases sterile copulations occurred twice before a fertile mating.

DISCUSSION

The data from fetal counts and ova counts support the hypothesis that much of the difference in litter size from PHH and PHL sires is attributable to a few litters in which PHH spermatozoa do not fertilize all of the ova. Also, there may be some difference in the number of resorptions.

Krzanowska (1964b) found a longer time interval between pairing and copulation in females of two inbred strains than in females of their F_1 hybrid. The data from C3H/He, PHH and PHL females indicate that some strains have been affected more than others by inbreeding in this respect.

IV. SPERM NUMBER, MORPHOLOGY AND MOTILITY

Differential staining of spermatozoa has been used to determine percentage of viability by Lasley, Easley and McKenzie (1942), Hancock (1951), and Beatty and Sharma (1960), among others. Beatty (1961) has stated that one of the best guides to fertility of a semen sample is the percentage of unstained sperm cells in a nigrosin-eosin preparation. Beatty and Sharma (1960) reported marked differences among strains for head breadth and area and for midpiece length. Braden (1958b) showed a strain difference in shape at the posterior end of the sperm head, the head tending to be angular in C57BL males, but smoothly rounded or slightly flattened in CBA males.

MATERIALS AND METHODS

Sperm from the vasa deferentia were obtained by stripping or flushing them out. After nigrosin-eosin slides were made, samples were taken for haemacytometer counts. Dimensions of spermatozoa on the nigrosin-eosin slides were obtained by means of an occular micrometer at a magnification of 970. In addition, spermatozoa from one male of each strain were compared by means of a microprojector. For preparation of nigrosin-eosin slides the suspension was spread immediately after a thorough mixing which required less than 30 seconds. The excess at one end of the slide was blotted, followed by air drying at 24°C. Venetian turpentine and a cover glass were then applied. Morphology of spermatozoa was studied by determining the percentage of spermatozoa having abnormally shaped heads and by taking measurements of the head and midpiece. Abnormalities of the head included missing acrosome, gross distortion of the shape, and cases in which the tip of the acrosome was bent back toward the base of the head.

To compare normal ejaculates, containing spermatozoa from the epididymis as well as from the vas deferens, ejaculated spermatozoa from the two strains were obtained. More than one ejaculate was obtained from some of the males to determine variation within males. There were 8 ejaculates from 4 PHH males and 7 from 4 PHL males. A second series of counts was made a year later at about the same time of year—November and December. Ages ranged from 191 to 335 days for PHL and from 178 to 311 for PHH males. Females in induced estrus were placed with males 11 hours after the HCG injection. Within ⅓ to 2 hours after copulation the female was killed, the entire reproductive tract removed, the uterus cut just above the plug, and the uterine contents flushed out by 1.0 ml physiological saline per uterine horn. For 16 out of 23 counts the time interval between copulation and examination did not exceed 40 minutes. In some cases 0.5 ml of physiological saline, followed by 0.5 ml of sodium citrate, per horn, were used instead of saline alone. Fluid remaining after flushing was expressed by means of forceps. After the nigrosin-eosin slides were prepared, live spermatozoa remaining in the solution were killed with a drop of formaldehyde. Two samples were taken for haemacytometer counts. For each sample spermatozoa were counted in each of five squares. After uterine spermatozoa were counted, oviducts were examined for spermatozoa up to 11 hours after copulation. Oviduct contents were obtained by flushing. The procedure was the same as that used to obtain ova. After the cumulus cells and ova had settled in the center of the depression slide, they were transferred by means of a narrow bore pipette to a microscope slide. A cover glass with a thin rim of vaseline all the way around was placed over the transferred material. Spermatozoa were examined by means of a phase contrast microscope and classified as normal or abnormal with respect to head morphology. In a later study of the proportion of bent (looped) spermatozoa entering the oviduct the spermatozoa were flushed directly onto the microscope slide.

RESULTS

The mean sperm count from vasa deferentia of eleven PHL males was 2,296,000 and that from eight PHH males was 1,597,000. The difference is not statistically significant. Counts of spermatozoa from the first series of ejaculates ranged from 1,750,000 to 11,700,000 per ejaculate for PHH males and from 250,000 to 8,850,000 for PHL males. For the second series counts for 3 ejaculates from 2 PHL males ranged from 2,875,000 to 8,250,000. Counts from two PHH males were 675,000 and none. One male from each strain in the first series had no spermatozoa in the ejaculate. No significant differences between PHH and PHL were detected. There were large variations within strains and even within the same male. Counts of the three ejaculates from the PHL male with the lowest count were 3,100,000; 250,000; and 3,000,000. No male was used twice within the same week, and the low count from this particular male came nearly 3 weeks after the last previous ejaculation.

The males used for ejaculates were tested for fertility before counts were made. In most cases fertilized ova were recovered from females following copulation, but some males had sired litters prior to the time the counts were made. Subsequently most males sired litters. The only exceptions were the two males in the first series (one PHH and one PHL) that had no spermatozoa in their ejaculates. The PHH males in the second series fertilized some but not all the ova when they were tested for fertility. Both males sired litters subsequent to the sperm counts, however.

The only measurement that showed a tendency toward difference between strains was the percentage of live spermatozoa (PHH 30±3.3, PHL 44±5.1 for spermatozoa from the vas deferens). Also, on numerous occasions when percentages of motile spermatozoa were estimated from haemacytometer counts the PHL males consistently provided a larger fraction of motile spermatozoa than comparable samples from PHH, and motility of PHL spermatozoa was more vigorous than that of PHH spermatozoa. Nigrosin-eosin stains made 4 and 8 hours after removal of spermatozoa from the vasa deferentia showed a higher percentage of viability of PHL compared to PHH spermatozoa. The difference seemed to be accentuated at these longer time intervals. The percentages of viable spermatozoa from the first series of ejaculates were 70 for PHH (range 43 to 84) and 77 for PHL (range 57 to 89).

Head and midpiece dimensions were the same for the two strains. There was no consistent difference in shape of the posterior end of the head. Seemingly normal spermatozoa from both strains have several variations in shape.

Percentages of morphologically abnormal spermatozoa for 8 ejaculates from PHH males were 41 (range 28 to 49) from the uterus and 17 (range 10 to 43) from the oviducts. Percentages for 7 ejaculates from PHL males were 45 (range 35 to 53) from the uterus and 20 (range 6 to 33) from the oviducts. Over half of the abnormal spermatozoa from some oviducts were still motile when examined. In most instances there were a number of spermatozoa which could not be classified as to morphology. Either the head was embedded in cumulus cells or it was turned sideways. Many of the spermatozoa that were embedded in cumulus cells were motile and omitting them may have led to an overestimate of percent abnormal. A lapse of time between flushing and classification might have the same effect, particularly since absence of acrosome was considered an abnormal condition.

Bent spermatozoa were seen in oviducts from all four females in which oviducal spermatozoa were found. In one female there were enough spermatozoa that a meaningful comparison could be made between percent of bent sperm in the uterus and in the oviducts. The ejaculate came from a PHL male. The average value for uterine spermatozoa that were bent at the posterior end of the midpiece was 6%. An average of 9% were bent at the neck immediately posterior to the head. These values were obtained from two nigrosin-eosin-stained smears and assumed that no bent spermatozoa straighten (or straight ones bend) as the smear is made. Corresponding values for the oviducts were 15/159=9% bent at the midpiece, and 3/159=2% bent at the neck.

In a study of ejaculates from males that lacked seminal vesicles spermatozoa were found in the oviduct when there were only 10,000 in the uterus. Perhaps this would be possible even with lower counts.

DISCUSSION

Krzanowska (1962) found differences in morphology and sperm counts among inbred, crossbred, and outbred males that differed in fertility, but no difference in percent of viable spermatozoa from the vasa deferentia. The situation seems to be different in PHH and PHL males. PHL compared to PHH males have a higher percentage of viable spermatozoa from vasa deferentia, but apparently do not differ in percentage of abnormal spermatozoa or sperm counts.

A study of the effect of various "t" alleles on fertility by Braden and Gluecksohn-Waelsch (1958) revealed no correlation between infertility and proportion of morphologically abnormal spermatozoa. Although many normal spermatozoa were ejaculated by infertile males, none of these spermatozoa were found in the distended portion of the ampulla (site of fertilization). Krzanowska (1962) reported that few abnormal spermatozoa traverse the mouse uterotubal junction and the abnormality of those that do is usually of rather mild form, affecting only the end of the acrosome. She suggested that some morphologically normal spermatozoa are not capable of fertilization. It seems safe to conclude from the data presented here that reduced fertility of PHH spermatozoa as compared with PHL is not caused by a proportionally higher number of morphologically abnormal spermatozoa ejaculated and transported to the site of fertilization. The data show that the uterotubal junction admits a lower proportion of morphologically abnormal than of normal spermatozoa. The values for percentage of abnormal spermatozoa are useful for comparing proportion of abnormal spermatozoa delivered to the uterus and to the oviducts, but the age range of males for both strains included ages at which, according to Beatty and Mukherjee (1963), there is an increase in proportion of spermatozoa with abnormal acrosome caps. Hence, the values cannot be compared with those found for other strains. Bent sperm seem capable of entering the oviduct. Viability of spermatozoa from the vas deferens is lower for PHH than for PHL males.

V. SUMMARY AND CONCLUSIONS

PHH spermatozoa fertilize relatively few of the available ova following artificial insemination. Competition with PHL spermatozoa seems to make PHH spermatozoa even less effective. The number of fertile inseminations and number of progeny per litter from PHH spermatozoa is higher in single than in double inseminations. Capacitation time seems not to be the reason. Slow penetration, particularly of the cumulus cells, may be partly responsible because: (1) the effectiveness of PHH spermatozoa is less when in competition with PHL; (2) PHH spermatozoa are more often successful when the interval between PHH and PHL inseminations is 69 minutes or more; (3) the effectiveness of PHH spermatozoa is slightly improved when hyaluronidase is injected with them. Compared with PHL spermatozoa a lower proportion of PHH spermatozoa (from the vas deferens) are viable and more of the viable spermatozoa are bent double.

Some ejaculates from PHH males fertilize only a few of the available ova. This may account for at least half the reduction in size of litters sired by PHH males. The effect of the low zygote counts on the mean number of normal zygotes is equivalent to the effect of small litters on litter size and on number of fetuses at 14 to 17 days gestation. More PHH males compared with PHL males have the tendency to fertilize only a few of the ova, and PHH males frequently fertilize none of the ova.

Failure of normal PHH spermatozoa to be transported to the oviduct does not seem to be responsible for the low fertility of PHH spermatozoa.

Since the function of PHH spermatozoa seems to be impaired and the percentage of normal, motile spermatozoa is low the variation among ejaculates, particularly the variation in number of sperm, may be sufficiently large to cause the occasional small litter and the more frequent sterile copulation. The required threshold for number of functional PHH spermatozoa is not always attained.

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THE UNIVERSITY OF KANSAS
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BIONOMICS AND ZOOGEOGRAPHY OF TIGER BEETLES OF SALINE HABITATS IN THE CENTRAL UNITED STATES (COLEOPTERA: CICINDELIDAE)

By

Harold L. Willis

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THE UNIVERSITY OF KANSAS
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Bionomics and Zoogeography of Tiger Beetles of Saline Habitats in the Central United States (Coleoptera: Cicindelidae)[1]

By

Harold L. Willis

INTRODUCTION

Cicindelids of saline habitats first came to my attention when, upon visiting a salt flat in Stafford County, Kansas, for the first time, in October 1961, I was amazed to find a species of tiger beetle *(Cicindela togata)* abundant on the barren, salt-encrusted soil. Further collecting in such habitats revealed that there are a number of species adapted for living in saline areas that are found nowhere else. It seemed worthwhile to investigate how these insects "make a living" in such harsh environments and how they came to be distributed and adapted to saline habitats scattered widely over the central United States.

A survey of the literature showed that although adults of North American cicindelids are quite well known taxonomically, relatively little work has been done on the life history, ecology, or zoogeography of most species. Shelford (1907, 1908, 1911, 1913d, 1917) and Criddle (1907, 1910) have done excellent work on the life cycles and ecology of a number of species in northeastern North America. Hamilton (1925) described the larvae of about 25 United States species and Spangler (1955) described another. Many other authors have made some mention of bionomics in addition to other subjects; Ortenburger and Bird (1933) are among the few to mention cicindelids of saline habitats in the central United States. Several general works with zoogeographical emphasis have included some or all cicindelids of the United

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[1] Contribution No. 1342 from the Department of Entomology, The University of Kansas, Lawrence, Kansas.

States (Horn, 1908-1915; Papp, 1952; Schilder, 1953b; Rivalier, 1950, 1954, 1957, 1961, 1963). Studies by Wickham (1904a, b), Cazier (1948, 1954), and Rumpp (1956, 1957, 1961), have included species of saline habitats of the southwestern United States and Mexico, a few of which also occur in the central United States. Except for brief habitat and distribution notes in many papers, these are the only works having any direct connection with the species in this study. Many of the minor works and others dealing with foreign species will be mentioned later.

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MATERIALS AND METHODS

As many saline habitats as possible in the central United States (southern Nebraska, Kansas, western Missouri, and Oklahoma) were visited during 1963-1965 to obtain specimens and data. Many were visited repeatedly to obtain information on seasonal distribution. When possible, large series of specimens were collected for statistical analysis. Both larvae and adults were collected alive and brought into the laboratory for life history studies.

In the laboratory, larvae were kept in tall jars full of soil from their natural habitat and were fed either small arthropods from weed sweepings or Mediterranean flour moths, *Anagasta kuehniella*, from a stock culture. Adults and young larvae resulting from their oviposition were kept in terraria partly filled with soil from saline habitats. A small Stender dish with water and a shelter made from a card with its corners bent down were provided, and the adults were given food similar to that offered the larvae. The temperature of the laboratory was a nearly constant 24.5°C, although occasionally a gooseneck lamp was placed over the terraria to provide more heat. The soil of the larval and adult containers was moistened occasionally. Eggs, pupae, and teneral adults were kept in Stender dishes for observation.

In addition to over 3600 specimens collected personally, over 15,400 specimens were borrowed from or examined at most of the major insect collections in the United States and Canada. More details about certain methods will be given later.

SALINE HABITATS

Saline terrestrial habitats are found throughout much of the world. The most widely distributed are coastal, including beaches, tidal flats, and salt marshes. Chapman (1960) has reviewed the extensive literature on coastal saline habitats. Coastal salt marshes are generally densely vegetated and thus unfit for cicindelids; however, tidal flats and beaches are often well populated.

Away from the coast, one may encounter inland saline habitats, which are not subjected to periodic inundation by tides or wave action. Inland saline and alkaline habitats are found in all continents, primarily in semiarid and arid regions. These inland areas are associated with three types of soil; one contains underground deposits of sodium chloride, another has excess sodium chloride and sodium sulfate in the surface layers, and the third has sodium sulfate, sodium carbonate, and/or magnesium sulfate in a subsurface layer. The soils with subsurface deposits are called alkali soils (Chapman, 1960). Richards (1954) defines a saline soil as one that contains an excess of soluble salts (the electrical conductance of a saturated paste in the unit of measure; the arbitrary value of 4 mmhos/cm is the lower limit of saline soils) and an alkali soil as having an excess of exchangeable sodium (15% exchangeable sodium is the lower limit of alkali soils). Soils with an excess of both soluble salts and exchangeable sodium are called saline-alkali soils. The pH of saline soils is ordinarily less than 8.5; that of alkali soils is above 8.5, sometimes reaching 10. The pH of saline-alkali soils is variable, but usually below 8.5 (Richards, 1954). The commonness of saline and alkaline habitats in arid and semiarid regions is due partly to the evaporation rate and low rainfall of such areas, which decrease the leaching of salts into the ground water where they can be carried away. Restricted drainage is another factor contributing to the salinization of soils; temporary or permanent flooding, as well as irrigation, may raise the ground water level and cause accumulation of salts at the surface (Richards, 1954). Alkalization of soil occurs by cation adsorption on the surfaces of soil particles as a consequence of electrical charges (Richards, 1954).

The original source of the salts is the minerals which weather out of the rocks of the earth's crust; however, a more direct source is from marine deposits of earlier geologic ages. The salts are usually moved by surface and ground water to areas in which they are concentrated.

Most saline habitats contain characteristic vegetation which has been variously classified. Chapman (1960) used the terms halophyte and glycophyte (mesophyte or non-halophyte), but said that one cannot always readily distinguish between them. Many halophytes exhibit characteristic physical modifications, such as a glaucous appearance, succulence, water storage hairs, small leaves, a glabrous surface, and salt-secreting glands (Chapman, 1960).

The vegetation of coastal and inland saline habitats is often very similar, often consisting of closely related species; however, there are greater differences from one continent to another. Both coastal and inland saline habitats often exhibit a zonation of vegetation, primarily in response to varying degrees of salinity, although other factors such as drainage and topography are important. Chapman (1960) reviewed many studies of this phenomenon. In coastal areas, a definite succession to mesic conditions has been found; however, Chapman (1960) said that in inland areas, the zonation is usually static and the vegetation must be considered an edaphic climax. Baalman (1965), in a study of a salt flat in Oklahoma, decided that little change in vegetation could be expected in highly saline areas. Ungar (1965) called the vegetation of a Kansas salt marsh a sub-climax which would change to a mesic climax if excess salts and water were removed.

Fewer studies have been made on the fauna of saline habitats. Davis (1962) surveyed the seasonal abundance of insects in North Carolina coastal salt marshes. Smalley (1960) studied the energy flow in populations of a Georgia salt marsh grasshopper, and Teal (1962) reported on energy flow in an entire Georgia salt marsh ecosystem. Ortenburger and Bird (1933), Jackson and Warfel (1933), and Williams (1954, in Baalman, 1965) studied the ecology of several Oklahoma salt flats. Lengerken (1929) did a detailed study of halophilic beetles of the coast of Germany. Pearse, Humm and Wharton (1942) studied the ecology of sand beaches in North Carolina.

The area here arbitrarily called the central United States (southern Nebraska, Kansas, western Missouri, and Oklahoma) has been variously subdivided by biologists and geographers. The system given in Kendall, Glendinning, and MacFadden (1958) seems adequate: the western three-fourths of Nebraska, the western two-thirds of Kansas, and the Oklahoma panhandle are in the Great Plains; the rest of Nebraska and Kansas, the northwestern half of Missouri, and central Oklahoma are in the Central Plains; southeastern Missouri and Oklahoma are in the Interior Uplands.

SALINE HABITATS OF THE CENTRAL UNITED STATES. Saline habitats of the central United States may be divided into two categories having ecological significance for tiger beetles: fluvial, or salty rivers and streams, and nonfluvial. The latter may be arbitrarily subdivided on the basis of size and moisture into small salt patches (usually dry), salt flats (dry or moist), salt marshes, and salt lakes. The two major categories may be in close contact or superimposed, as when salty patches occur next to saline streams or when drainage streams cross large salt flats.

The distribution of saline habitats in the central United States is somewhat irregular. The larger ones occur in a broad band running obliquely from southwestern Oklahoma through central Kansas to southeastern Nebraska. Smaller habitats occur in central and northeastern Oklahoma, southeastern

Kansas, and north-central Missouri. In the central United States, such habitats are usually far isolated from one another compared to parts of the southwestern United States. They are of both natural and man-made origin. In northern Kansas and southern Nebraska, the salt comes from deposits in upper Dakota shales (Cretaceous), while in southern Kansas and northern Oklahoma, the gypsum redbeds (Permian) and Cretaceous strata are responsible (Ungar, 1965; Baalman, 1965). In oil-producing areas, small salty patches or small salt flats frequently occur where brine has been released during drilling. The major oil producing areas of the central United States are found in southeastern and central Kansas and central Oklahoma (Moore and Haynes, 1917; Redfield, 1927).

The man-made saline areas can be dated relatively well. Oil was found in Kansas in 1860, soon after its discovery in Pennsylvania, but most drilling was not done in Kansas and Oklahoma until the late 1800's and early 1900's (Moore and Haynes, 1917; Gould, 1930); thus these saline habitats are not over 80 or 90 years old. Natural saline areas north of the limits of Pleistocene ice (Wright and Frey, 1965) have obviously not existed in their present condition before this time. Frye and Leonard (1952) stated that the present Kansas landscape is a product of erosion and deposition during the Pleistocene.

In pollen analyses of sites in Meade County, Kansas, and Harper County, Oklahoma, Kapp (1963) and Stephens (1959), respectively, concluded that these areas were similar to the present eastern Dakotas or moderate elevations in the southern Rockies during the Illinoian glacial period. Today these areas are short grass prairie.

The physical and chemical conditions of saline habitats are often extreme, particularly at the level at which insects live. Salinity varies greatly with the season (less in spring when most rain occurs), depth (higher at surface), and topography, but may reach as high as 3% (Unger, 1965); when the weather is dry, a white encrustation of crystalline salt usually occurs on the surface. Because of this variability and since tiger beetles occur in most parts of saline habitats, salinity was not measured in this study.

Temperature may be extreme on the bare or sparsely vegetated surface of saline habitats. Geiger (1965) stated that in the summer the surface temperature of bare soil may reach 60, 70, or even 80°C. Above or below the surface the temperature drops rapidly. A study by Sinclair (*in* Geiger, 1965, and Allee *et al*., 1949) in Tucson, Arizona, showed that the soil just below the surface reached 71.5°C, was 62.5°C at a depth of 2 cm, dropped to 42.2°C at 10 cm, and was 20°C at 60 cm; meanwhile the air temperature in a standard shelter was 42.5°C. Also, the daily range of temperatures was greatest near the surface (56.5°C) and less below (40.1°C at 2 cm, 13.8°C at 10 cm, 0°C at 60 cm) or above (31.5°C) the surface. Occasionally measurements of soil and air temperature taken in this study gave similar results; surface temperatures much greater (5-13°C) than air temperatures were frequently noted. Geiger (1965) also stated that a vegetational cover may have a moderating effect on temperature, but what vegetation does occur in saline habitats is usually low and sparse and would have little effect (Geiger said that in grass under a meter high, the maximum temperature is still at the surface).

The availability of water varies considerably with the season as well as with the type of habitat. In rainy weather, saline habitats may be quite moist or flooded, but during the hot, dry months of July and August the surface may become very dry and hard. The salinity of available water varies widely, depending on its origin, and may reach 3% (Ungar, 1965). Humidity also varies greatly; Ortenburger and Bird (1933) noted that the relative humidity on a salt flat at Cherokee, Oklahoma, varied from 80 or 90% in the morning to 20 or 30% at midday.

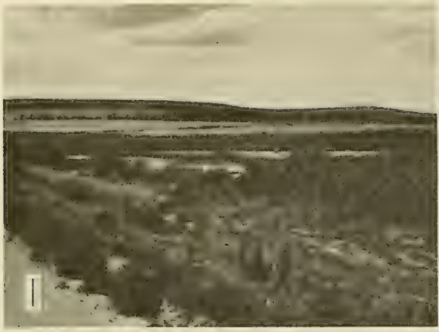
Wind velocity, usually high in prairies anyway, is especially great on the wide, bare expanses of salt flats. In the summer months the wind normally blows steadily from the south, and on salt flats in southern Kansas and northern Oklahoma, I have estimated the maximum velocity to be 40 to 50 miles per hour during fair weather. Fluvial habitats are usually more protected from wind. The strong wind not only has a physical effect important to flying insects but also has a marked desiccating effect.

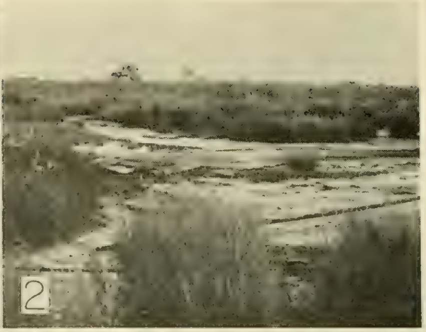
Another characteristic of many saline habitats is the general lack of or low amount of cover which would allow insects to escape many of the above conditions as well as predators and parasites.

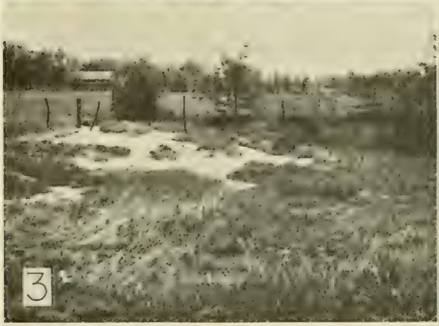
The vegetation of saline habitats in the central United States is primarily affected by variations in local topography, drainage, and salinity (Ungar, 1965). In most habitats there is an area of very high salinity (2-3%) where no flowering plants occur. In areas of less salinity (up to 2.75%), *Distichlis stricta*, a low, wiry grass, and *Suaeda depressa*, a sparse, succulent chenopod, are the dominant plants. In more marginal and less saline areas, *Atriplex patula* (Chenopodiaceae), *Sporobolus airoides*, *Poa arida*, *Hordeum jubatum*, *Spartina pectinata* (Gramineae), and *Tamarix gallica* (Tamaricaceae, an introduced woody shrub) occur along with the above-mentioned species. Many other species are less common, although some (*Salicornia*, Chenopodiaceae) become dominant species farther west in the United States. More complete analyses of the vegetation of two saline habitats in Kansas and Oklahoma can be found in Ungar (1964, 1965) and Baalman (1965).

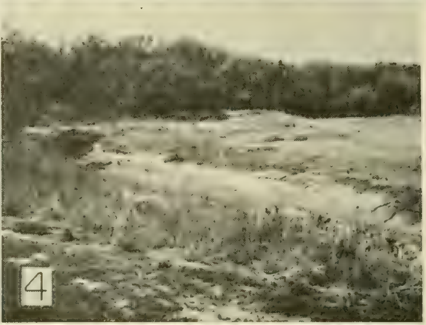
On many saline habitats, low mounds or hummocks have been formed by the pioneering vegetation (*Distichlis* and *Suaeda*) collecting blowing sand or soil at their bases. These hummocks may continue to grow, reaching heights of a meter or more in some cases, and allow normal prairie flora and fauna to inhabit their tops (Ortenburger and Bird, 1933; Baalman, 1965).

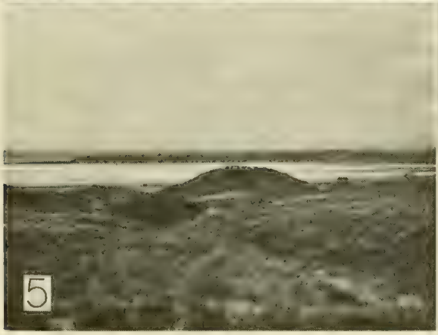
Some typical saline habitats visited in this study are shown in Figures 1-8.

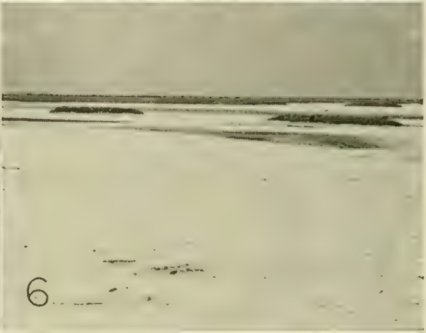


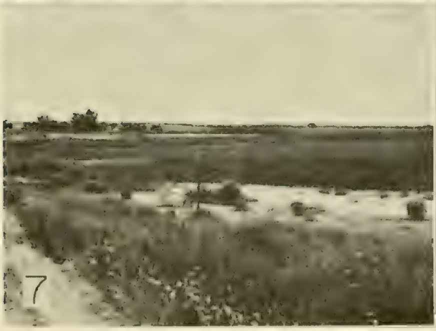












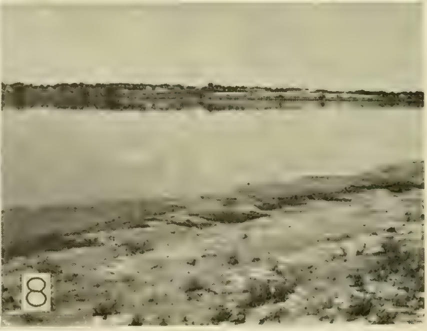


Fig. 1. Small salty patches in corner of plowed field, 11 m. north, 1 mi. east of Lincoln, Lincoln Co., Kansas (17 June 1963). Fig. 2. Small salt flat near oil wells, 2 mi. north, ½ mi. east of Chanute, Neosho Co., Kansas (18 August 1964). Fig. 3. Small salty patches near Salt Creek, 1 mi. northwest of Fredonia, Wilson Co., Kansas (20 April 1963). Fig. 4. Small intermittent creek with salty banks, 5 mi. north of Yates Center, Woodson Co., Kansas (20 April 1963). Fig. 5. Large (8 miles long, 2 miles wide) salt flat on the Cimarron River, 2.5 mi. southwest of Plainview, Woods Co., Oklahoma (29 August 1963). Fig. 6. Large hummocks on salt flats, Great Salt Plains National Wildlife Refuge, 3 mi. east of Cherokee, Alfalfa Co., Oklahoma (27 August 1963). Fig. 7. Salt marsh with cattails and sedges in area of greatest moisture, ½ mi. east, 1 mi. south of Talmo, Republic Co., Kansas (18 June 1963). Fig. 8. Salt Lake, with bare salty patches around shore, Lincoln, Lancaster Co., Nebraska (19 June 1963).

For the purposes of this paper, most saline habitats can be divided into a central bare, nonvegetated area and a sparsely vegetated marginal area (including the margins of the islandlike hummocks), although in some, the marginal vegetation is tall and dense.

INTRODUCTION TO *CICINDELA*

The genus *Cicindela*[2] is found in terrestrial habitats throughout most of the world from about 50° south latitude to the Arctic Circle, except for high mountains and many midoceanic islands. Except for the closely related monotypic genera *Eurymorpha* and *Apteroessa*, *Cicindela* is considered to be the most highly evolved genus in the family Cicindelidae (Horn, 1926). Many species of *Cicindela* throughout the world live in saline habitats, and many of these are not closely related, hence the ability to live in such habitats has apparently evolved independently a number of times. In general, however, species of saline habitats are among the more highly evolved species of the genus.

Considering the North American fauna of *Cicindela*, many of the more advanced species (the arrangement of Rivalier, 1954, is being followed, with slight modifications) live in saline habitats exclusively, and a sprinkling of less advanced species occur in such habitats occasionally or exclusively. The cicindelids found in saline habitats of the central United States include some species found only in such habitats and some found in both mesic and saline habitats with more or less equal frequency. The species included in this study, with brief notes on their habitat and distribution, are listed in Table 1. As one moves outside the area here arbitrarily called the central United States, other species may be encountered in saline habitats. Some of the species in Table 1 that are primarily found in mesic habitats are relatively uncommon in the habitats studied, and others have been or are being more thoroughly studied by others. Therefore, this study is concentrated on the following species: *C. circumpicta*, *C. cuprascens*, *C. fulgida*, *C. macra*, *C. nevadica*, *C. togata*, and *C. willistoni*. In addition, certain other species which are closely related to these will be briefly considered.

BIONOMICS OF *CICINDELA*

The following account is based on observations of several species. Most of the work on the life history was done with *C. togata*, but *C. circumpicta*, *C.*

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[2] A number of workers have suggested splitting *Cicindela* into a variable number of genera. The most recent and best arrangement to date is in a series of papers by Rivalier (1950-1963) based primarily on the male genitalia. This proposal has met some opposition; many workers feel that Rivalier's "genera" should be treated as subgenera. I shall follow the latter viewpoint in this work.

TABLE 1. Species of *Cicindela* included in this study, types of habitats in which they occur, and their general distribution (F=fluvial, N=nonfluvial).

C. circumpicta La Ferté; N (sometimes F) saline habitats; N. Dak., Neb., Mo., Kans., Colo., Okla., N. Mex., Tex., Tamaulipas (Mexico).

C. cuprascens LeConte; F mesic and saline habitats; Manitoba (Canada), Mont., Wyo., Colo., N. Mex., Tex., La., Miss., Ala., Tenn., Ky., Ohio, Ind., Ill., Ia., Minn., and areas enclosed within this circle.

C. duodecimguttata Dejean; F mesic and saline habitats; Northwest Terr. Alberta, Sask., Manitoba, Ontario, Quebec, Labrador, Newfoundland, Nova Scotia, and N. Brunswick (Canada), south to Ga., Ala., Miss., Ark., Tex., Colo., Wyo., Mont., and areas enclosed within this circle.

C. fulgida Say; N saline habitats; Alberta, Sask., and Manitoba (Canada), N. Dak., Mont., S. Dak., Wyo., Neb., Colo., Kans., N. Mex., Okla., Tex., Ariz.

C. hirticollis Say; F mesic and saline habitats; Brit. Col., Alberta, Sask., Manitoba, Ontario, Quebec, Newfoundland, Prince Edw. Is., and N. Brunswick (Canada), most of continental United States, Baja Calif., Chihuahua, and Vera Cruz (Mexico).

C. macra LeConte; F mesic and saline habitats; Ohio, Ky., Tenn., La., Tex., Colo., Wyo., Neb., S. Dak., Minn., Wisc., Mich., and areas enclosed within this circle.

C. nevadica LeConte; F and N saline (sometimes mesic) habitats; Sonora and Coahuila (Mexico), Calif., Nev., Ariz., Ut., N. Mex., Tex., Okla., Colo., Kans., Neb., Wyo., S. Dak., Mont., N. Dak., Sask. and Manitoba (Canada).

C. punctulata Olivier; N (sometimes F) mesic and saline habitats; Alberta, Sask., Manitoba, and Ontario (Canada), most of continental United States except Pacific Northwest and Calif., Sonora, Chihuahua, Coahuila, Durango, Zacatecas, Hidalgo, Puebla, Distrito Federal, and Mexico (Mexico).

C. repanda Dejean; F and N mesic and saline habitats; Brit. Col., Alberta, Sask., Manitoba, Ontario, Quebec, Labrador, Newfoundland, N. Brunswick, and Nova Scotia (Canada), most of continental United States except Southwest.

C. schauppi G. Horn; N saline and mesic habitats; Okla., Tex., Nuevo Leon (Mexico).

C. togata La Ferté; N (sometimes F) saline habitats; Neb., Kans., Colo., Okla., N. Mex., Tex., La., Miss., Ala., Fla., S. Car., Tamaulipas (Mexico).

C. tranquebarica Herbst; N mesic and saline habitats; Northwest Terr., Brit. Col., Alberta, Sask., Manitoba, Ontario, Quebec, N. Brunswick, Nova Scotia, and Prince Edw. Is. (Canada), most of continental United States.

C. willistoni LeConte; N (sometimes F) saline habitats; Calif., Nev., Ore., Ut., Ariz., Wyo., N. Mex., Tex., Okla., Kans.

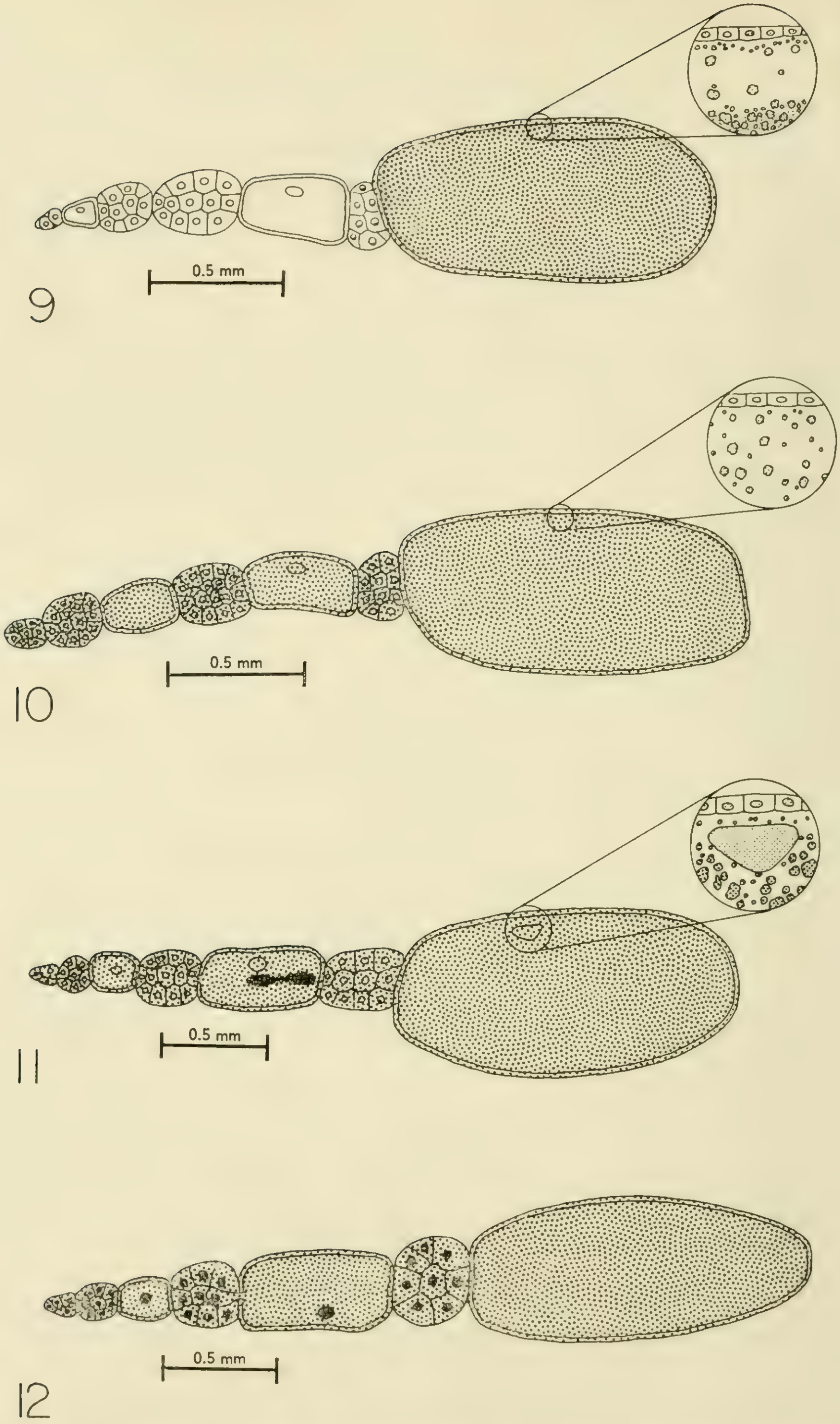
fulgida, and *C. nevadica* were also studied. Nearly all the species in Table 1 were considered from the ecological viewpoint. This account will consider each stage of the life cycle separately. The following brief summary, taken mostly from Balduf (1935), will serve as an introduction to the bionomics of *Cicindela* in general.

The eggs are laid in the soil; the newly hatched first instar larva enlarges the hole produced by the adult's ovipositor into a burrow. Burrows are usually perpendicular to the surface, more or less straight, and with the opening flush with the surface. The three larval instars lie in wait at the entrance to their burrows for prey, the head and pronotum forming a camouflaged "plug" to the burrow. Most small arthropods are accepted as food and are taken to the bottom of the burrow to be consumed unless they are too large for the diameter of the burrow. The last instar larva digs a special pupal cell in which transformation to the adult occurs. The adult digs its way out and spends most of its active hours hunting prey or reproducing. Small arthropods are the usual food. Adults usually prefer open, sparsely vegetated areas and are most active during warm, sunny weather. The female carefully selects the type and moisture of the soil used for oviposition. The length and type of life cycle varies with the species. In some, the adults emerge in the fall, hibernate, and then mate and oviposit in the spring, dying during the summer; in others, the adults emerge during the summer and die before winter. The larval stage occupies most of the life cycle, which may take one to four years to complete.

THE EGG. Since most adult *Cicindela* are about the same size, the eggs of most species are probably very similar. Shelford (1908) said that the eggs of *C. purpurea* and *C. repanda* are about 2 mm long and 1-1.5 mm wide, a translucent creamy yellow, and larger at the anterior end. Moore (1906) gave similar sizes for two eggs of *C. repanda*, but judging from his descriptions, they were apparently atypical and shrunken. Huie (1915) said that the eggs of the European *C. campestris* are 2 mm long, oval, smooth, and yellowish when laid. Ponselle (1900) found the eggs of *C. flexuosa* to be 2 mm long and 1 mm wide.

I found the eggs of *C. circumpicta*, *C. duodecimguttata*, *C. nevadica*, and *C. togata* to be similar. The mean length and width of 38 eggs of *C. togata* measured with an eyepiece micrometer was 2.08 x 1.01 mm; the ranges were 1.85 - 2.43 x 0.92 - 1.12 mm. The average size of four eggs of *C. circumpicta* was 2.21 x 0.99 mm. One egg of *C. duodecimguttata* was 1.80 x 1.14 mm, and a desiccated *C. nevadica* egg was 1.70 x 0.74 mm. Eggs will absorb water and swell slightly if placed in a moist environment. The eggs examined were ovoid and not much larger at the anterior end than the posterior. There is sometimes a slightly concavity on the ventral side. The chorion is shiny, but under high magnification a fine reticulate pattern can be seen. The chorion is not very strong, and the egg is easily ruptured. When first laid, the egg is a creamy or light straw yellow and filled with yolk granules. In *C. togata*, the posterior end of the egg is attached to the soil at the bottom of the hole made by the ovipositor by a short stalk of sticky material (Fig. 13). In *C. circumpicta*, no definite stalk was seen, but the egg adhered to the soil because its posterior end was sticky. Moore (1906), Huie (1915), and Zikan (1929) also noted that *Cicindela* eggs are sticky or fastened by a stalk.

Histological sections of the ovaries of *C. togata* were made and stained



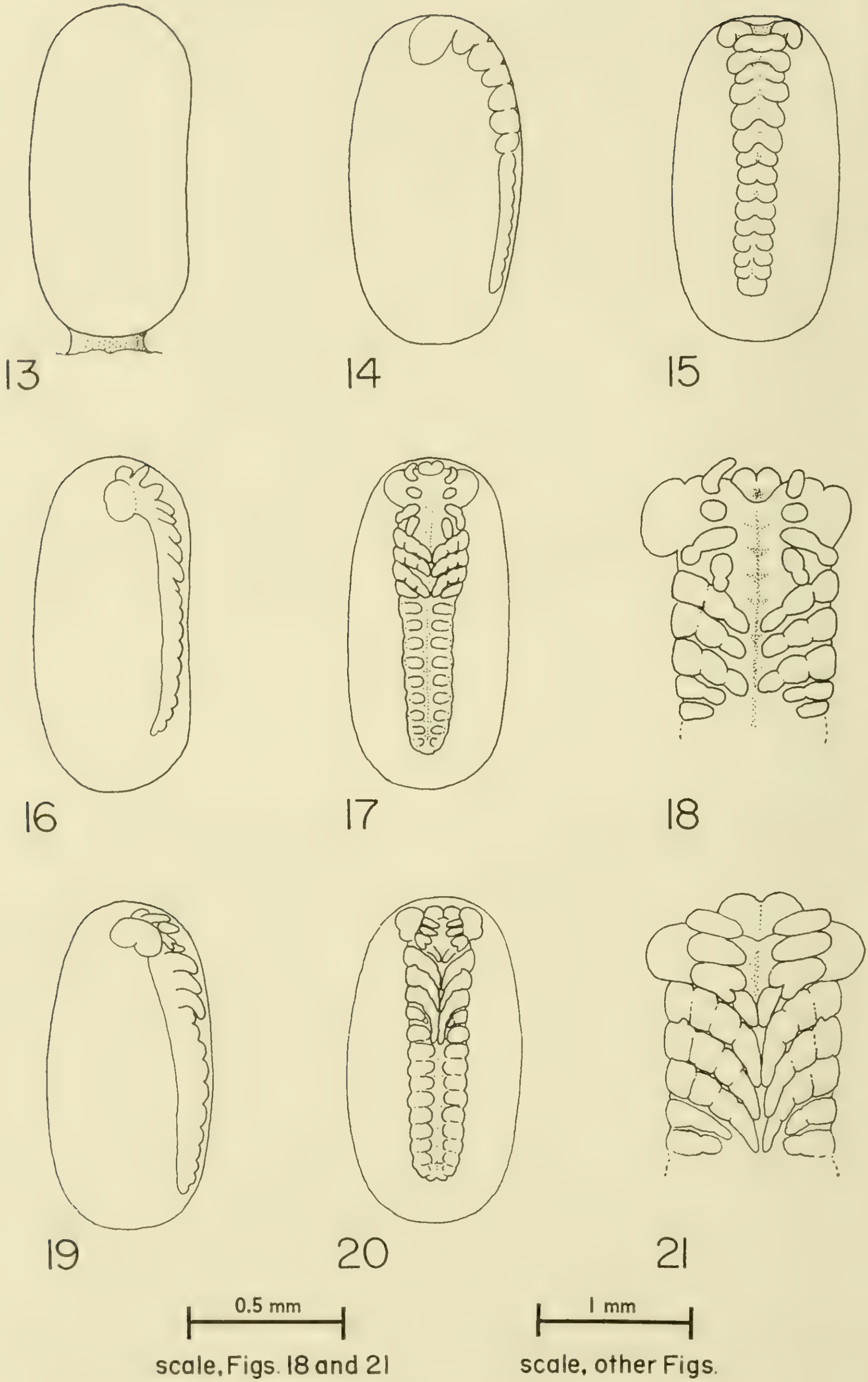
Figs. 9-12, ovary of *C. togata*, longitudinal section; Fig. 9, stained according to the periodic acid—Schiff procedure; inset: enlargement of the peripheral cytoplasm of the terminal oocyte; areas stained are shaded. Fig. 10, stained according to the azo-coupling protein method; inset: enlargement of the peripheral cytoplasm of the terminal oocyte; areas stained are shaded. Fig. 11, stained according to the Sudan black B method for lipids; inset: enlargement of the peripheral cytoplasm and female pronucleus of the terminal oocyte; areas stained are shaded. Fig. 12, stained according to the methyl green-pyronin Y method for nucleoproteins; areas stained are shaded: black=green, stipple=purple-red.

according to the following methods: the periodic acid-Schiff (PAS) procedure (Barka and Anderson, 1963) for gylcogen, muco- and glycoproteins, glycolipids, mucopolysaccharides, and simple proteins; the azo-coupling protein method (Barka and Anderson, 1963) for proteins in general; the Sudan black B method (Pearse, 1960) for lipids; and the methyl green-pyronin Y method (Pearse, 1960) for nucleoproteins. The results are shown in Figures 9-12. The ovaries of cicindelids are of the polytrophic meroistic type, as are those of all Adephaga (with follicles of nurse cells, or trophocytes, alternating with follicles of oocytes). In Figures 11 and 12, nutrient material can be seen entering oocytes from trophocytes.

In Figure 9, it can be seen that PAS-positive nutrients do not enter the oocyte until very late, since only the terminal oocyte is stained. An enlargement of it shows a layer of cytoplasm near the vitelline membrane with few stained granules. All cells are lightly stained by the azo-coupling reaction (Fig. 10), which is not surprising, since all cells contain proteins. In the terminal oocyte, relatively few granules contain protein. In the Sudan black B lipid reaction (Fig. 11), the cytoplasm of all cells is stained, and the nuclei are only very lightly stained. In the oocyte of intermediate development, a dense-staining central core is present, indicating that most of the lipids have entered the oocyte or have been synthesized within it by this time. This may be the same as the corelike "polar vitelline granules" of Hirschler (1932). In the terminal oocyte, different sized granules are stained in varying degrees, and the nucleus is stained to a greater degree than in other oocytes. In the methyl green-pyronin Y reaction, DNA stains green and RNA stains purple-red. In Figure 12, the nuclei of all cells stained green and the cytoplasm purple-red, as expected.

EMBRYOLOGICAL DEVELOPMENT. The gross embryology of *C. togata* was studied. Fragmentary observations on *C. circumpicta* and *C. duodecimguttata* were similar to those made on *C. togata* and will not be discussed. Almost no work has been done on the embryology of cicindelids. Shelford (1908) published a small drawing of an embryo of *C. purpurea* within the egg and stated that the egg hatches in about two weeks. Huie (1915) mentioned that more mature eggs of *C. campestris* exhibit two pairs of eyes through the chorion. Zikan (1929) said that embryological development takes 9-29 days, depending on the species and temperature (he studied other genera of cicindelids as well as *Cicindela*; the genera *Ctenostoma* and *Odontochila* take about one month).

Eggs of *C. togata* were recovered from terrarium soil in which adults had oviposited. When possible, eggs were dug up just after oviposition. The eggs were kept individually in small covered Stender dishes in which a small amount of water was placed to avoid desiccation. They were examined under a dissecting microscope with transmitted light twice a day. The laboratory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14
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0.5 mm
scale, Figs. 18 and 21
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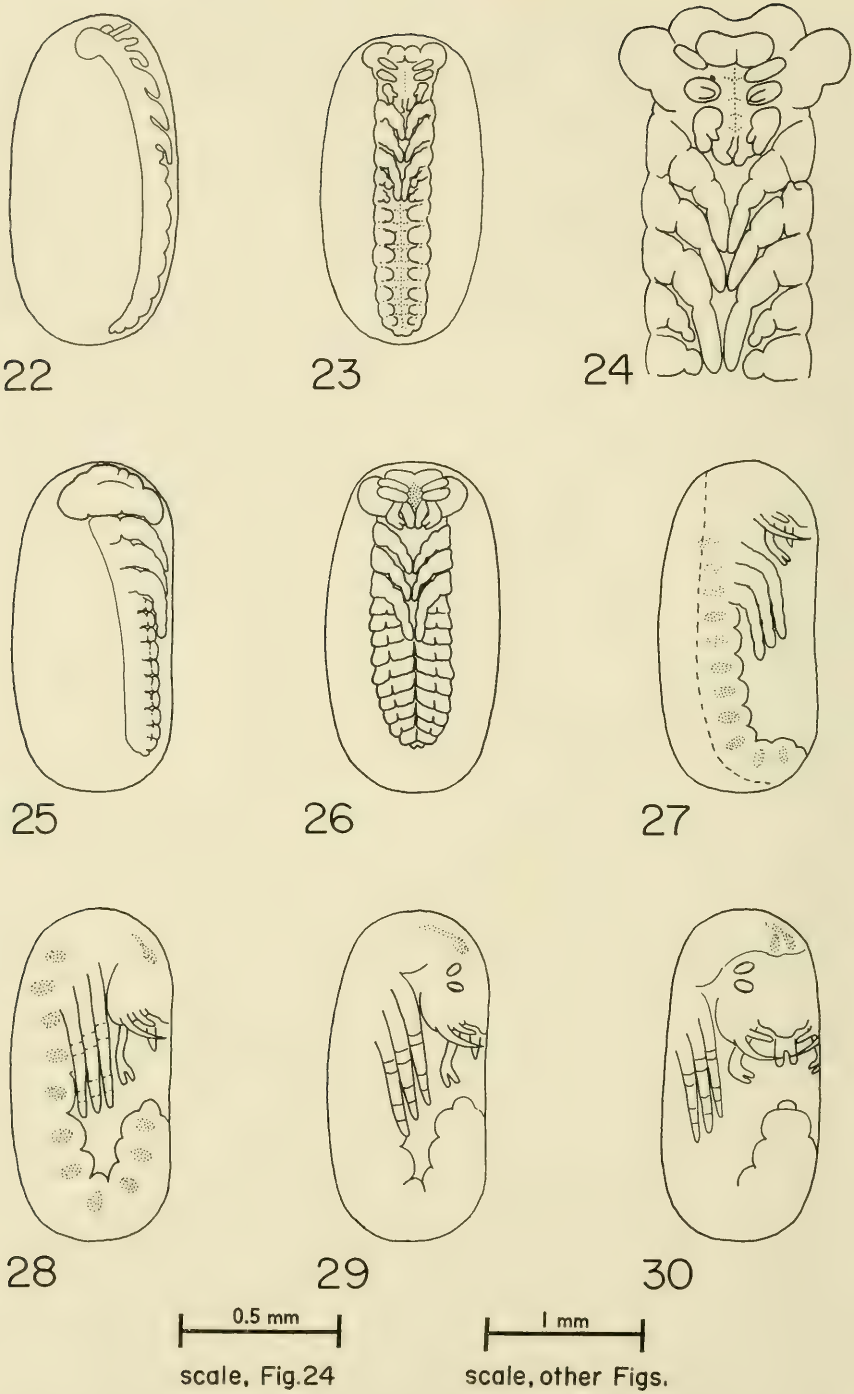
FIG. 13. Newly laid egg of *C. togata*, showing stalk at its posterior end attaching it to the substrate. FIGS. 14-21, embryos of *C. togata*; FIG. 14, early embryo (about 1 day old), lateral aspect; FIG. 15, same, ventral aspect; FIG. 16, about 2 days old, lateral aspect; FIG. 17, same, ventral aspect; FIG. 18, same, enlargement of anterior portion; FIG. 19, about 2.5 days old, lateral aspect; FIG. 20, same, ventral aspect; FIG. 21, same, enlargement of anterior portion.

temperature was 24.5°C. The transparent chorion makes eggs of *Cicindela* ideal for such observations. In addition, the embryos of fixed eggs were dissected out and examined.

The gross embryological development of *C. togata* is shown in Figures 13-34. The newly laid egg (Fig. 13) is filled with homogeneous appearing yolk granules. Such features as the cleavage center and cleavage nuclei could not be seen. As can be seen in the histological sections (Fig. 11), the female pronucleus is located near the periphery on one side. After about one day, the yolk in the anterioventral portion of the egg appears less dense than the rest (in live eggs). Presumably the germ band and germ layers are being formed or have been formed by this time. Then follow several stages that have been observed only in fixed eggs. Figures 14 and 15 show an early embryo. Head and thoracic segmentation are well developed, and abdominal segmentation is nearly complete. Only four segments can be seen in the head region, the apical one being composed of the paired lateral lobes. A median line, or primitive groove, is just beginning to develop midventrally. At a later stage (Figs. 16-18), the lateral lobes of the head are much enlarged; four pairs of head appendages (antennae, mandibles, maxillae, and labium) plus a median bilobed labral bud are clearly visible; the maxillae and labium are beginning to segment; what is probably the stomodeum can be seen as a depression at the base of the labral bud. The thoracic and first abdominal appendages are quite long and are beginning to segment; other abdominal appendages are mere bumps. The median line is clearly evident. At a slightly later stage (Figs. 19-21), the head appendages have enlarged and thickened; the maxillae are beginning to become bilobed; the labial appendages have moved closer together. The thoracic and first abdominal appendages are clearly segmented, and the other abdominal appendages are beginning to segment. The legs are longer. The fifth abdominal segment is slightly larger in diameter than those surrounding it. Slightly later (Figs. 22-24), the head appendages have elongated; the mandibles begin to assume their future scimitar shape; the outer lobes of the maxillae have elongated considerably; what may be the anterior tentorial pits can be seen at the bases of the mandibles when the antennae are straightened out. The first abdominal appendage is three-segmented, and the other abdominal appendages are slightly two-segmented. At this stage the early embryo has reached maximum elongation. Later, when the embryo is about three to four days old (Figs. 25, 26), the lateral lobes of the head have enlarged greatly; the maxillae have assumed a characteristic L shape. The legs are longer, but the body is shorter and wider. The abdominal appendages have begun to regress. Returning to observations of living eggs, Figure 27 shows a stage slightly more advanced (4 to 5.5 days old) than that in Figures 25 and 26. The amount of yolk has decreased considerably; the embryo has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23
24
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27
28
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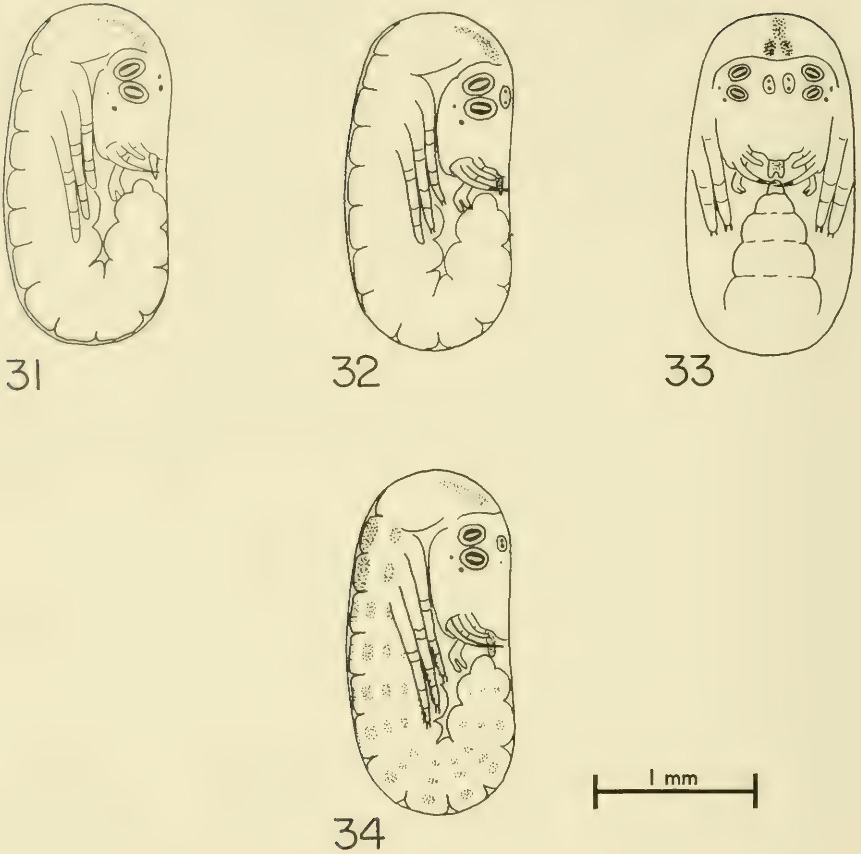
30
0.5 mm
scale, Fig.24
1 mm
scale, other Figs.

Figs. 22-30, embryos of *C. togata*; Fig. 22, about 3 days old, lateral aspect; Fig. 23, same, ventral aspect; Fig. 24, same, enlargement of anterior portion; Fig. 25, about 3.5 days old, lateral aspect; Fig. 26, same, ventral aspect; Fig. 27, about 4-5.5 days old, lateral aspect; Fig. 28, about 5-6.5 days old, lateral aspect; Fig. 29, about 7-9 days old, lateral aspect; Fig. 30, same, ventrolateral aspect.

moved dorsally; and the abdomen is beginning to flex ventrally. The mandibles are much elongated and clearly sickle-shaped, and the L-shaped, bilobed maxillae are much longer. Dark segmental "spots" can be seen internally in the thorax and abdomen. A paired pulsating organ appears in the anterior region of the prothorax. During the next day, the body continues to elongate, forcing the head and abdomen closer together (Fig. 28). The abdomen may be seen moving slightly. At an age of 7 to 9 days, the body is slightly longer, and two pairs of large developing stemmata become visible as very faint orange ovals on either side of the head (Figs. 29, 30). A tubular pulsating area can be seen extending posteriorly through the thoracic region from the paired organ near the head. The internal segmental "spots" are no longer visible. Probably the dorsal closure is completed by this stage. In another day (8 to 10 days days after oviposition), the large ovals representing developing stemmata have become thicker and dark orange; three additional pairs of smaller stemmata become visible as faint gray dots, two pairs mesad of the large pairs and one pair laterad of the most posterior large pair; the large pairs of developing stemmata are surrounded by transparent circles. The dorsal segmentation can be clearly seen. What appears to be the labium becomes light orange (Fig. 31). The entire embryo may move slightly in this and subsequent stages. About one day later (Figs. 32, 33), the small pairs of stemmata are darker gray, and another pair is beginning to develop laterad of the posterior large pair; the median pairs of small stemmata have transparent circles around them. The labium is dark orange; the tips of the mandibles (but not the extreme tips) are orange; the tarsal claws of the first legs are orange and those of the second legs light orange. A few hours to one-half day later (Fig. 34), the stemmata mentioned above are darker orange (large ones) or gray (small ones); the two pairs of medial stemmata have begun to fuse (the anterior ones with the posterior) and each fused pair is surrounded by a common transparent circle; another medial pair of stemmata is visible posterior to the fused pairs as very light gray dots. The orange of the mandibles has spread slightly; the tarsal claws of the second legs are orange, and those of the third legs are light orange. Sclerites of the legs, thorax, and abdomen are very light gray; the setae at the apical ends of the legs are dark. When development reaches this stage, the larva bursts the chorion at the anterior end and in about five minutes, wiggles out. The duration of embryological development, measured in four individuals, is from 10.5 to 11.25 days under laboratory conditions (temperature 24.5°C).

The Larva—*Descriptions.* The larvae of cicindelids are relatively little known, either biologically or taxonomically. A number of workers have described many of the palearctic species, and the larvae of some tropical genera are known. Among the more important papers for these regions are van Emden (1935, 1943), Zikan (1929), Friederichs (1931), Blair (1920), Hamil-



FIGS. 31-34, embryos of *C. togata*; FIG. 31, about 8-10 days old, lateral aspect; FIG. 32, about 9-11 days old, lateral aspect; FIG. 33, same, ventral aspect; FIG. 34, just before eclosion, lateral aspect.

ton (1925), and Gilyarov and Sharova (1954). In North America, G. Horn (1878) described one species in each of the four North American genera; Schaupp (1879a) listed the species that had been described at that time; Shelford (1908) described rather superficially the larvae of 12 species; Hamilton (1925) described in detail 28 North American and six palearctic species of *Cicindela*, three species of *Megacephala*, three species of *Omus*, one species of *Amblychila*, and two species of tropical genera, and standardized the morphological terminology; Ortenburger and Bird (1933) published crude drawings of the larva of *C. willistoni* and the fifth abdominal segment of the larvae of *C. cuprascens* and *C. togata*; Spangler (1955) described the larva of *C. circumpicta*, but his drawings do not show some important details and are incorrect in others.

In this study, the larvae of six species were collected; four were identified by rearing and two *(C. fulgida* and *C. willistoni)* by the process of elimination. One of these, *C. duodecimguttata*, has been adequately described by Hamilton (1925) and will not be described here; the larvae of *C. togata*, *C. nevadica*, *C. fulgida*, and *C. willistoni* are described for the first time, and *C. circumpicta* is redescribed. See Hamilton (1925) for an explanation of morphological terminology. Descriptions of larval cicindelids have traditionally been based on last instar larvae, no doubt partly because of a scarcity of specimens of younger instars. I shall follow this convention, although I have also collected or reared first and second instar larvae of most of the species described here.

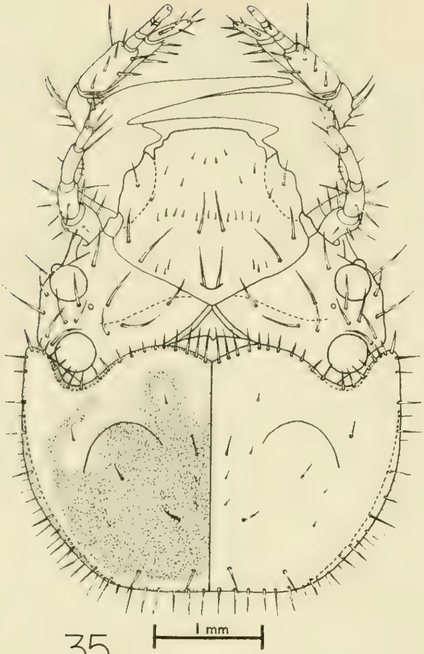
Larvae will be deposited in the following institutions: U.S. National Museum (all five species), American Museum of Natural History (all species except *C. fulgida*), and The University of Kansas (all species except *C. fulgida* and *C. willistoni*).

C. circumpicta johnsoni Fitch—third instar larva (Figs. 35-40)

Color. Head cupreous, cupreous-green, brassy green, or blue, with green, blue-green, blue, or purple reflections; labrum red-brown with black margin; pronotum with most of disk chestnut brown in a pattern which may be more or less developed (Fig. 35); cephalolateral angles yellow-brown to yellow; mesonotum dark brown anteriorly, yellow-brown posteriorly; metanotum yellow-brown; basal two antennal segments yellow-brown, distal segment reddish brown, penultimate segment intermediate; mandibles reddish brown basally with apices and retinaculum black; maxillae and labium yellow-brown. Dorsal cephalic and pronotal setae transparent, other setae yellow-brown.

Head. Setae on dorsum medium in length and prominent; diameter of stemma II subequal to that of stemma I and slightly greater than distance between I and II; fronto-clypeo-labral area slightly wider than long; U-shaped ridge on caudal part of frons with 2 setae; antennae with distal segment 0.85 as long as penultimate, proximal segment slightly longer than second segment, proximal segment with 6-7 setae, second with 7-9, third with 3-4, and distal with 3-5; maxillae with 3 setae on mesal margin of proximal segment of galea and 4-5 on distal segment; maxillary palpus 3-segmented, palpifer with 7 setae, penultimate segment with 2 setae; distal segment of labial palpus with 1 ventral seta, penultimate with 3 spurs and 2 setae on either side of spurs; ligula with 4 setae.

Thorax. Pronotum with cephalolateral angles extending as far cephalad as mesal portion; lateral margins slightly carinate; primary setae medium in length; secondary setae few, 5 or 6 pairs.



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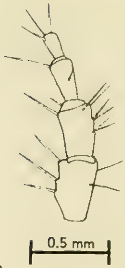

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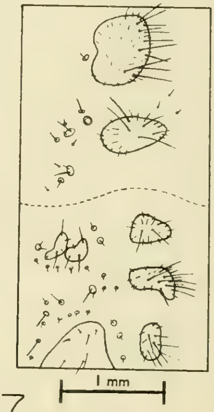

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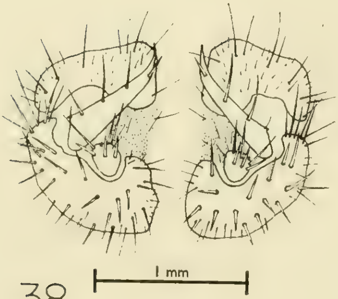

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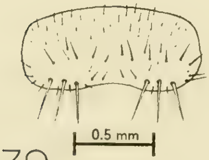

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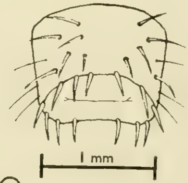

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Figs. 35-40, *C. circumpicta johnsoni*, third instar larva; specimen is from Geuda Springs, Sumner Co., Kansas; Fig. 35, head and pronotum, dorsal aspect; left half of pronotum shaded to show the pattern; Fig. 36, left antenna, ventral aspect; Fig. 37, third abdominal segment, lateral aspect of left half, with the middorsal line at top and midventral line at bottom; ventrolateral suture dotted; Fig. 38, dorsum of fifth abdominal segment, dorsal aspect; stippled area is weakly sclerotized; Fig. 39, ninth abdominal sternum, ventral aspect; Fig. 40, pygopod, dorsal aspect.

Abdomen. Sclerotized areas distinct, supplementary lateral sclerotized areas variable in number and shape; secondary setae numerous, some long and slender, some short and fine; eusternum of ninth segment bearing 2 groups of 3 long setae caudally; pygopod usually bearing 14 setae, 7 on a side; median hooks of fifth segment with 4-5 (rarely 6) setae, the distal one stout and directed mesad, the others more slender and directed laterad; inner hooks with 6-8 setae, 3-5 of which are notably stouter than the others; spine of inner hooks minute to obsolete.

Measurements. Total length of larva, 16-21 mm; width at third abdominal segment, about 2 mm; diameter of stemma I, 0.34-0.38 mm; diameter of stemma II, 0.27-0.37 mm; distance between stemmata I and II, 0.21-0.30 mm; length of fronto-clypeo-labral area, 1.5-1.7 mm; width of fronto-clypeo-labral area, 1.56-1.80 mm; length of pronotum, 1.93-2.19 mm; width of pronotum, 2.93-3.25 mm.

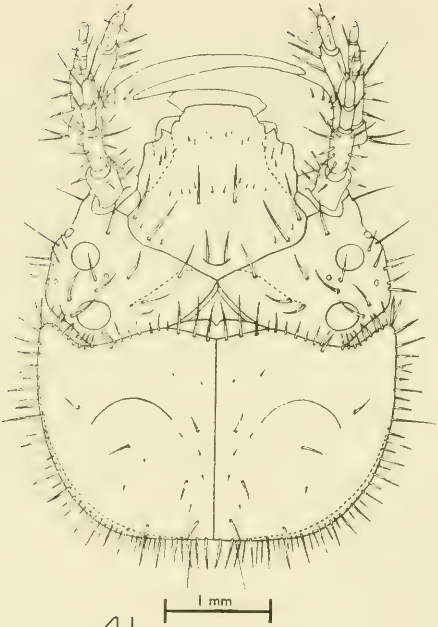
C. fulgida fulgida Say—third instar larva (Figs. 41-46)

Color. Head red-brown with brassy green and cupreous-purple reflections; labrum red-brown with black margin; pronotum brown or dark red-brown with cupreous-purple reflections; cephalolateral angles lighter brown; mesonotum dark brown anteriorly, yellow-brown posteriorly; metanotum yellow-brown; antennae red-brown; mandibles red-brown basally with apices and retinaculum black; maxillae and labium yellow-brown. Dorsal cephalic and pronotal setae white, other setae yellow-brown.

Head. Setae on dorsum medium in length; diameter of stemma II noticeably smaller than that of stemma I and smaller than distance between I and II; fronto-clypeo-labral area slightly longer than wide; U-shaped ridge on caudal part of frons with 2 setae; antennae with distal segment 0.7 as long as penultimate, proximal segment shorter than second segment; proximal segment with 5-6 setae, second with 9, third with 2, and distal with 3-4; maxillae with 3 setae on mesal margin of proximal segment of galea and 5 on distal segment; maxillary palpus 3-segmented, palpifer with 7 setae, penultimate segment of palpus with 2 setae; distal segment of labial palpus with 1 ventral seta, penultimate with 3 spurs and 2 setae on either side of spurs; ligula with 4 setae.

Thorax. Pronotum with cephalolateral angles extending cephalad slightly more than mesal portion; lateral angles carinate; primary setae medium in length; secondary setae few, 7 or 8 pairs.

Abdomen. Sclerotized areas distinct; secondary setae numerous, most long and slender, a few short; eusternum of ninth segment bearing 2 groups of 3 long and 1 shorter seta caudally; pygopod usually bearing 18 setae, 9 on a side; median hooks of fifth segment with 2 setae; inner hooks with 2 setae on a shoulder and long spine over one-third the length of the hook.



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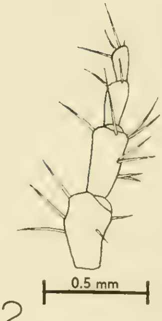

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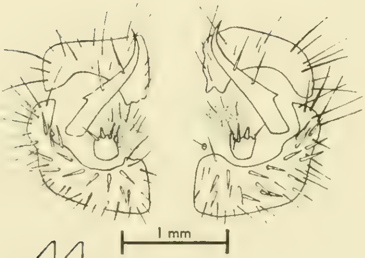

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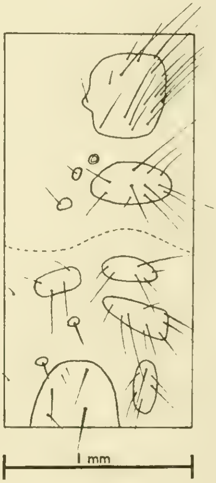

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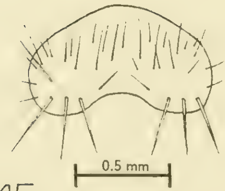

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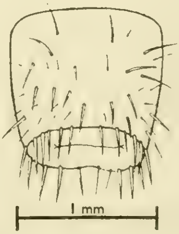

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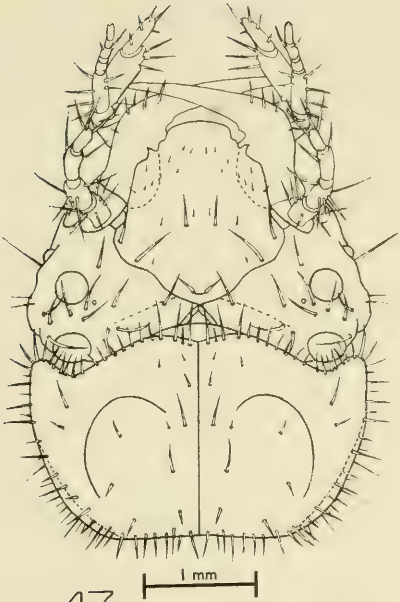
Figs. 41-46, *C. fulgida fulgida*, third instar larva; specimen is from 11 mi. northeast of Hudson, Stafford Co., Kansas; Fig. 41, head and pronotum, dorsal aspect; Fig. 42, left antenna, ventral aspect; Fig. 43, third abdominal segment, lateral aspect of left half; ventrolateral suture dotted; Fig. 44, dorsum of fifth abdominal segment, dorsal aspect; stippled area is weakly sclerotized; Fig. 45, ninth abdominal sternum, ventral aspect; Fig. 46, pygopod, dorsal aspect.



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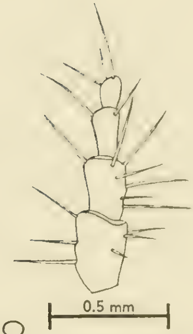

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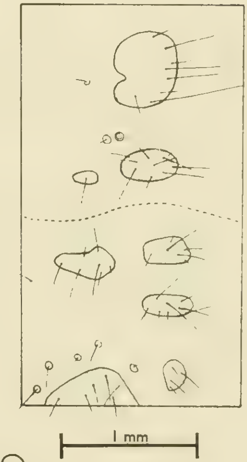

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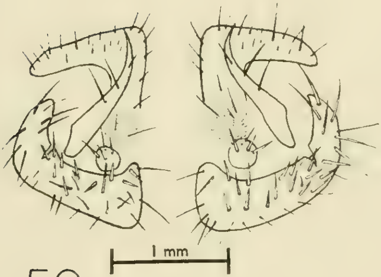

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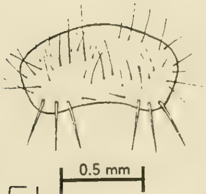

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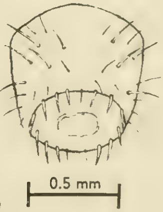

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FIGS. 47-52, *C. nevadica knausi*, third instar larva; specimen is from 11 mi. northeast of Hudson, Stafford Co., Kansas; FIG. 47, head and pronotum, dorsal aspect; FIG. 48, left antenna, ventral aspect; FIG. 49, third abdominal segment, lateral aspect of left half; ventrolateral suture dotted; FIG. 50, dorsum of fifth abdominal segment, dorsal aspect; stippled area is weakly sclerotized; FIG. 51, ninth abdominal sternum, ventral aspect; FIG. 52, pygopod, dorsal aspect.

Measurements. Total length of larva, 14-18 mm; width at third abdominal segment, 1.7 mm; diameter of stemma I, 0.30 mm; diameter of stemma II, 0.26 mm; distance between stemmata I and II, 0.28 mm; length of fronto-clypeo-labral area, 1.48 mm; length of pronotum, 1.83 mm; width of pronotum, 2.95 mm.

C. nevadica knausi Leng—third instar larva (Figs. 47-52)

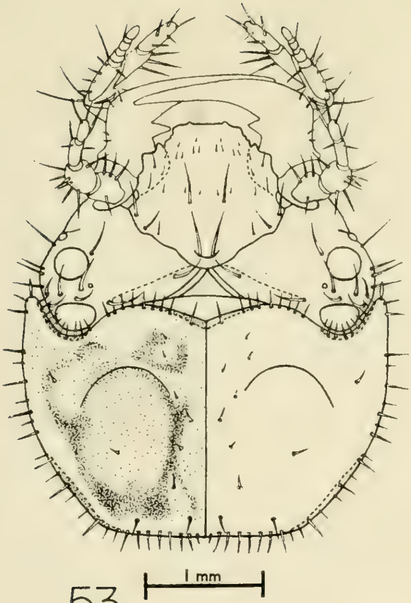
Color. Head black with metallic blue-green, green, purplish, or sometimes bronze reflections; labrum red-brown; pronotum with cephalolateral angles red-brown and disk black with purple, blue-green, brassy, and cupreous reflections; mesonotum dark brown anteriorly, yellow-brown posteriorly; metanotum yellow-brown; antennae reddish brown; mandibles reddish brown basally with apices and retinaculum black; maxillae and labium yellow-brown. Dorsal cephalic and pronotal setae transparent, other setae yellow-brown.

Head. Setae on dorsum prominent, long to short; diameter of stemma II subequal to that of stemma I and greater than distance between I and II; fronto-clypeo-labral area slightly wider than long; U-shaped ridge on caudal part of frons with 2 setae; antennae with distal segment 0.6 as long as penultimate; proximal and second segments about equal in length; proximal segment with 6-9 setae, second with 8-9, third with 2, and distal with 3; maxillae with 3 setae on mesal margin of proximal segment of galea and 5 on distal segment; maxillary palpus 3-segmented, palpifer with 7 setae, penultimate segment of palpus with 2 setae; distal segment of labial palpus with 1 ventral seta, penultimate segment with 2 large and one reduced spur and two setae on either side of spurs; ligula with 3 setae.

Thorax. Pronotum with cephalolateral angles not extending as far cephalad as mesal portion; lateral margins slightly carinate; primary setae long to short; secondary setae few, 4 to 6 pairs.

Abdomen. Sclerotized areas distinct; secondary setae few, some very long and slender, some medium in length; eusternum of ninth segment bearing 2 groups of 3 long and 1 shorter seta caudally; pygopod usually bearing 14 setae, 7 on a side; median hooks of fifth segment with 3-4 setae, all of about the same diameter; inner hooks with 4-5 setae, 3 of which are notably stouter than the others; spine of inner hooks minute to obsolete.

Measurements. Total length of larva, 18-20 mm; width at third abdominal segment, about 2 mm; diameter of stemma I, 0.31-0.33 mm; diameter of stemma II, 0.27-0.33 mm; distance between stemmata I and II, 0.22-0.26 mm; length of fronto-clypeo-labral area, 1.42 mm; width of fronto-clypeo-labral area, 1.44-1.48 mm; length of pronotum, 1.57-1.72 mm; width of pronotum, 2.43-2.63 mm.



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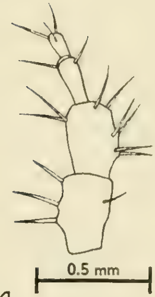

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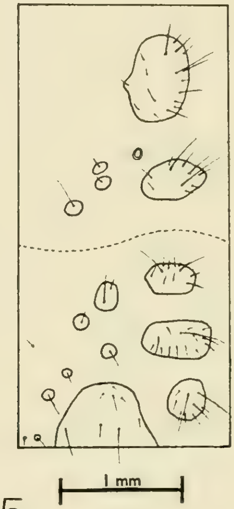

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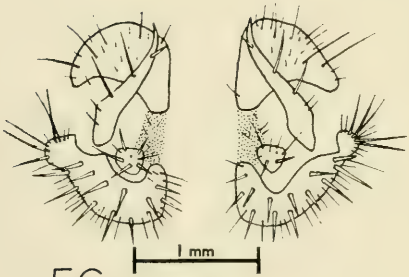

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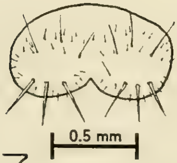

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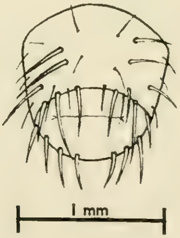

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Figs. 53-58, *C. togata globicollis*, third instar larva; specimen is from 11 mi. northeast of Hudson, Stafford Co., Kansas; Fig. 53, head and pronotum, dorsal aspect; left half of pronotum shaded to show pattern; Fig. 54, left antenna, ventral aspect; Fig. 55, third abdominal segment, lateral aspect of left half; ventrolateral suture dotted; Fig. 56, dorsum of fifth abdominal segment, dorsal aspect; stippled area is weakly sclerotized; Fig. 57, ninth abdominal sternum, ventral aspect; Fig. 58, pygopod, dorsal aspect.

C. togata globicollis Casey—third instar larva (Figs. 53-58)

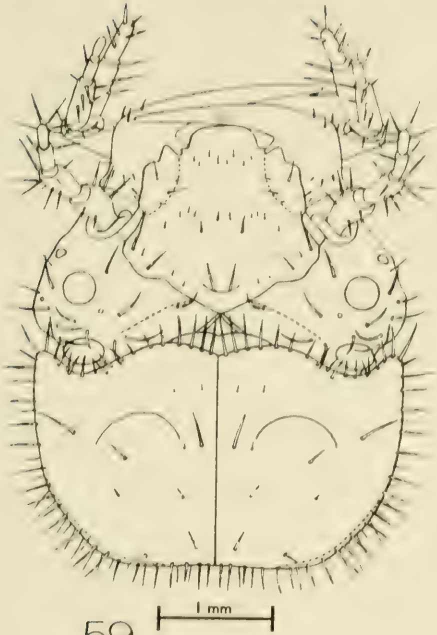
Color. Head cupreous and green with green reflections; labrum red-brown with 2 opalescent white spots and black margin; angulus frontalia opalescent white; pronotum with white margin, disk with pattern of red-brown to yellow-brown on yellow-brown to yellow background, which may be more or less developed (Fig. 53); mesonotum dark brown anteriorly, yellow-brown posteriorly; metanotum yellow-brown; basal two antennal segments opalescent white, distal two segments yellow-brown; mandibles reddish brown basally, with apices and retinaculum black; maxillae and labium yellow-brown. Dorsal cephalic and pronotal setae transparent, other setae yellow-brown.

Head. Setae on dorsum short and prominent; diameter of stemma II subequal to that of stemma I and slightly greater than distance between I and II; fronto-clypeo-labral area wider than long; U-shaped ridge on caudal part of frons with 2 setae; antennae with distal segment 0.57 as long as penultimate, proximal segment equal in length to second segment; proximal segment with 6 setae, second with 8-9, third with 3, and distal with 3; maxillae with 3 setae on mesal margin of proximal segment of galea and 5 on distal segment; maxillary palpus 3-segmented, palpifer with 7 setae, penultimae segment of palpus with 2 setae; distal segment of labial palpus with 1 ventral seta, penultimate with 3 spurs and 3 setae on either side of spurs; ligula with 4 setae.

Thorax. Pronotum with cephalolateral angles extending cephalad as far as or slightly beyond mesal portion; lateral margins slightly carinate; primary setae short; secondary setae few, 2 to 4 pairs.

Abdomen. Sclerotized areas distinct, supplementary lateral sclerotized areas variable in number and shape; secondary setae fairly numerous, some long and slender, some short and fine; eusternum of ninth segment bearing 2 groups of 3 long setae caudally; pygopod usually bearing 12 setae, 6 on a side; median hooks of fifth segment with 4-5 setae, the distal one stout and directed mesad, the others more slender and directed laterad; inner hooks with 5-8 setae, 3-5 of which are notably stouter than the others; spine of inner hooks minute to obsolete.

Measurements. Total length of larva, 17-19 mm; width at third abdominal segment, about 1.9 mm; diameter of stemma I, 0.32-0.35 mm; diameter of stemma II, 0.27-0.34 mm; distance between stemmata I and II, 0.23-0.27 mm; length of fronto-clypeo-labral area, 1.28-1.35 mm; width of fronto-clypeo-labral area, 1.42-1.50 mm; length of pronotum, 1.83-2.08 mm; width of pronotum, 2.85-3.20 mm.



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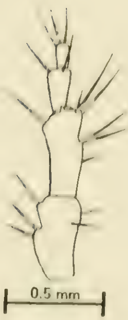

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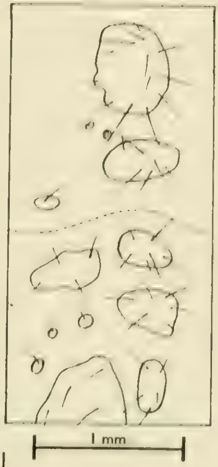

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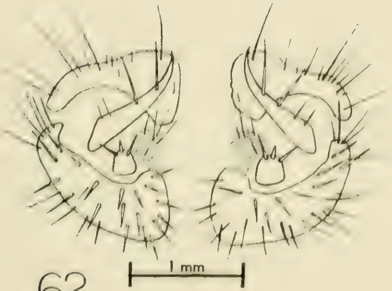

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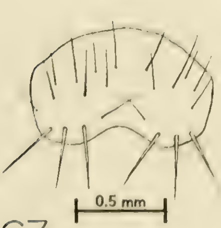

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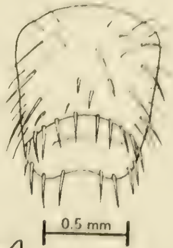

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FIGS. 59-64, *C. willistoni*, new subspecies, third instar larva; specimen is from 11 mi. northeast of Hudson, Stafford Co., Kansas; FIG. 59, head and pronotum, dorsal aspect; FIG. 60, left antenna, ventral aspect; FIG. 61, third abdominal segment, lateral aspect of left half; ventrolateral suture dotted; FIG. 62, dorsum of fifth abdominal segment, dorsal aspect; stippled area is weakly sclerotized; FIG. 63, ninth abdominal sternum, ventral aspect; FIG. 63, pygopod, dorsal aspect.

C. willistoni, new subspecies, described later—third instar larva (Figs. 59-64)

Color. Head dark brown to red-brown with brassy, green, blue-green, or purplish reflections; labrum red-brown; pronotum with disk usually dark red-brown (rarely red-brown in a pattern), with cephalolateral angles red-brown (rarely yellow-brown); mesonotum dark brown anteriorly, yellow-brown posteriorly; metanotum yellow-brown; basal two antenna segments red-brown to yellow-brown, distal two segments red-brown; mandibles reddish brown basally, with apices and retinaculum black; maxillae and labium yellow-brown. Dorsal cephalic and pronotal setae white, other setae yellow-brown.

Head. Setae on dorsum medium to short and prominent; diameter of stemma II subequal to that of stemma I and slightly greater than distance between I and II; fronto-clypeo-labral area about as wide as long; U-shaped ridge on caudal part of frons with 2 setae; antennae with distal segment 0.6 to 0.7 as long as penultimae; proximal segment shorter than second segment; proximal segment with 5-6 setae, second with 9-10, third with 2, and distal with 3; maxillae with 3 setae on mesal margin of proximal segment of galea and 5 on distal segment; maxillary palpus 3-segmented, palpifer with 7 setae, penultimate segment of palpus with 1 seta; distal segment of labial palpus with 1 ventral seta, penultimate segment with 3 spurs and 2 setae on either side of spurs; ligula with 4 (occasionally 6) setae.

Thorax. Pronotum with cephalolateral angles not extending as far cephalad as mesal portion; lateral margins slightly carinate; primary setae medium to short, secondary setae few, 3 to 4 pairs.

Abdomen. Sclerotized areas distinct, secondary lateral sclerotized areas variable in shape; secondary setae few, some long, some short; eusternum of ninth segment bearing 2 groups of 3 long and 1 shorter seta caudally; pygopod usually bearing 16 setae, 8 on a side; median hooks of fifth segment with 3-4 setae; inner hooks with 2 setae on a shoulder, spine long, over one-third the length of the hook.

Measurements. Total length of larva, 18 mm; width at third abdominal segment, about 2.3 mm; diameter of stemma I, 0.30-0.35 mm; diameter of stemma II, 0.27-0.34 mm; distance between stemmata I and II, 0.24-0.35 mm; length of fronto-clypeo-labral area, 1.42-1.70 mm; width of fronto-clypeo-labral area, 1.42-1.76 mm; length of pronotum, 1.66-2.02 mm; width of pronotum, 2.56-3.03 mm.

The larvae of *C. fulgida* and *C. willistoni* are segregated to couplet 7 in Hamilton's (1925) key; they can be separated from the species in that couplet by the following key:

1. Setae of dorsum of head and pronotum brown .... *sexguttata*
   Setae of dorsum of head and pronotum white 2

2. Median hooks of fifth abdominal segment with two setae .... *fulgida*
   Median hooks of fifth abdominal segment with more than three setae 3
3. Antennal scape shorter than pedicel .... *willistoni*
   Scape and pedicel of antenna subequal in length .... *campestris*

The larvae of *C. circumpicta*, *C. nevadica*, and *C. togata* are segregated to couplet 24 in Hamilton's (1925) key; they can be separated from the species in that couplet by the following key:

1. Inner hooks of fifth abdominal segment with nine or ten setae .... *marginata*
   Inner hooks of fifth abdominal segment with fewer than nine setae 2
2. Scape and pedicel of antenna opalescent white .... *togata*
   Scape and pedicel of antenna brown 3
3. Antennal pedicel with ten to 12 setae .... *abdominalis*
   Antennal pedicel with fewer than ten setae 4
4. Cephalolateral angles of pronotum not extending as far cephalad as mesal portion; pronotum less than 2.7 mm wide .... *nevadica*
   Cephalolateral angles of pronotum extending as far cephalad as mesal portion; pronotum more than 2.8 mm wide .... *circumpicta*

THE LARVA—*Bionomics*. Many brief notes and papers have appeared concerning the bionomics of cicindelid larvae, some of which will be mentioned later. Among the more important are Zikan's (1929) large paper on South American species, Shelford's (1908) paper, Huie's (1915) work on *C. campestris*, Friederich's (1931) detailed study of eyes, and two papers by Criddle (1907, 1910).

Sclerotization. The first instar larva of *C. togata*, upon hatching, is about 3 mm long. The body is light straw yellow except for the tips of the mandibles and the large stemmata, which are orange, and the meso- and metathoracic, abdominal, and leg sclerites and the small stemmata, which are light gray. The two hind pairs of legs are slightly darker gray than the front legs. After about four hours the above mentioned sclerites are darker gray, and the dorsum of the head and parts of the pronotum are gray. The gray of the mandibles has spread basally to about half their length. In about six more hours, the body sclerites are gray-brown, and the top of the head is dark and iridescent cupreous and green. The venter of the head is light brown. The mandibles are almost entirely black. In about 15-24 hours after eclosion, the larva is complete sclerotized. The abdominal sclerites are light gray-brown; the thoracic and leg sclerites (except the pronotum) are dark gray-brown; the pronotum is light yellow-brown with a darker brown pattern; the dorsum of the head is dark brown with cupreous and green reflections; the venter of the head is orange-brown; the mandibles are black; and the other head appendages are light-brown.

Burrows and digging. In nature, after the first instar larva is sclerotized, and if the soil is moist enough, it enlarges the cell that contained the egg into a burrow. Shelford (1908) said that the larva of *C. purpurea* first digs the burrow from the depth of the egg to the surface, then digs beneath this to a depth of 10-15 cm. The exact method of digging the first burrow was not determined in this study. The effect of soil moisture was noted in the laboratory terraria. Soil that had begun to dry out was watered, and shortly afterward numerous first instar larval burrows began to appear. If the soil becomes too dry again, the larva plugs the burrow with soil, apparently to conserve moisture.

In digging a burrow, the larva (of all instars; third instars are described here), head downward, loosens some soil with its mandibles, using its legs for support. Then the anterior end of the body is bent around in the other direction, and the head and pronotum are placed shovellike under the loose soil. The larva finishes turning right-side-up in the burrow and elevates the soil up the burrow on top of its head and pronotum. Upon reaching the surface, the larva may flip its head and pronotum backward, throwing the soil several centimeters away (if the soil is moist and sticky, it is deposited in the form of small pellets). Some species pack the soil around the entrance of the burrow by turning the head upside down and pushing with the legs. When the larva is beginning a burrow from the surface, as when it is introduced into a jar of soil in the laboratory, slightly different tactics are used. The thorax is humped, the larva supported by its front and especially hind legs (the middle legs are normally held horizontally from the body to help support the larva in the center of the burrow and are useless for walking when it is outside the burrow), in order to allow the mandibles, which slant upward from the head, to dig into the soil. When the hole is about 1 cm deep, the larvae may hold the abdomen in the air while using the legs to gain leverage. The larva uses the method of digging upside down and backing out the hole to flip the soil away until the hole is about 2 cm deep. At depths below that, the method of turning around in the burrow, described above, is used. The temporary bottom of the burrow is made slightly larger than the finished diameter; soil is later "plastered" on the walls as the burrow descends. When the burrow is completed, the larva clears the soil around the entrance of all movable obstructions within a distance of about half its body length, forming a slightly concave smooth area. Some of the same observations on digging have been made by Criddle (1907), Fackler (1918), Enock (1903), and Macnamara (1922). Shelford (1908) noted an exception: the burrow entrance of *C. macra* is ragged at the edge, rather than smooth. Some authors (Macnamara, 1922; Bryson, 1939) have noted an increase in burrowing activity after rains, and Criddle (1907, 1910) noted that most digging is done at night except late in the season when the nights are cold.

The depth of the burrow varies with many factors, including the instar, species, weather and climate, season, soil moisture, and possibly type of soil.

Shelford (1908) gave depths of (presumably) third instar burrows of eight species ranging from 5-90 cm, depending on the species, temperature, and possibly soil moisture. Criddle (1907, 1910) gave depths for six species ranging from 15-200 cm, depending on the instar, species and season (larvae deepen their burrows before hibernation). Zikan (1929) showed burrow depths of the species he studied. The depths of burrows measured in this study are shown in Table 2.

TABLE 2. Depths of larval burrows measured (in cm.) in the field (F) and laboratory (L).

	Instar		
Species	First	Second	Third
C. circumpicta	6.5-9 (F)	13.5-16.5 (F)	11-29.5 (F) 6-14 (L)
C. duodecimguttata	1.5-3.5 (F) 2-2.6 (L)	3.5-4.5 (F) 4 (L)	6-11 (L)
C. fulgida		13 (F)	
C. nevadica		18-28 (F)	22-35 (F)
C. togata	2.5-4 (F) 5 (L)	6.5-10 (F)	10-18 (F) 10-35 (L)
C. willistoni	7-13 (F)	12 (F)	16-35 (F)

The diameter of most larval burrows is slightly greater than the diameter of the head and pronotum, although Zikan (1929) and Williams and Hungerford (1914) showed the terminal part of the burrows of some species of other genera as being enlarged, and Shelford (1911) showed a similar burrow of *C. limbalis.* The larva can easily turn around inside the burrow. In doing this it bends the anterior end of the body dorsally using the legs, forcing the head past the dorsum of the abdomen (Shelford, 1911).

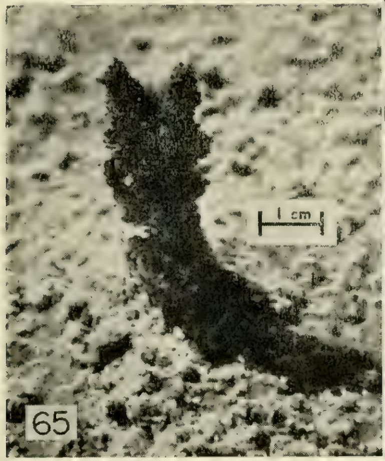
The burrows of most species are approximately straight and perpendicular to the soil surface, which may be vertical, horizontal, or oblique. However, there are many exceptions and much intraspecific variation. Burrows that I have dug up in the field or laboratory are aften curved, oblique to the surface, or both. Such variations have also been shown by some of the above authors as well as Hood (1903). Reineck (1923) noted that the larvae of *C. silvicola* will dig around large obstructions in their path.

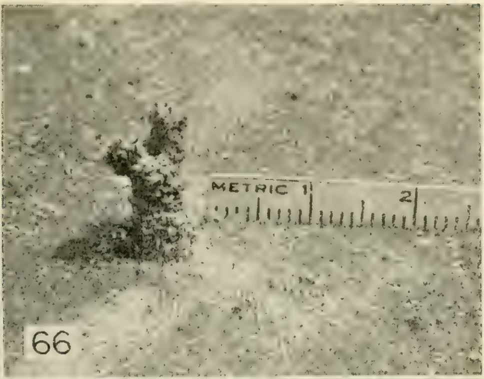
The burrows of many species open flush with the surface or with a slight depression as noted above, but others are quite different. Shelford (1908) noted that the burrow of *C. lepida*, which is found in dry sand, has a funnel at the entrance formed by the action of gravity on the sand. Ortenburger and Bird (1933) noted similar craterlike entrances to burrows of *C. cuprascens.* Shelford (1908) and Criddle (1910) found that *C. formosa* builds a pit about 4 cm wide and 2.5 cm deep. From about half way up one side, the burrow begins horizontally, then curves downward. Similar burrows were noted by Dow (1916) for four species, including *C. lepida* and *C. scutellaris*. However, he did not collect larvae for identification, but used the uncertain method of placing wire screen cages over the burrows to catch the emerging adults (uncertain because the adult does not necessarily dig its way out along the old larval burrow; larval burrows of different species may be close together, and the adult from one may emerge near another). Dow's determinations are thus in doubt, since Shelford (1908) and I have noted different burrow entrances for *C. lepida* and *C. scutellaris*, respectively.

Lesne (1897, 1921) and Reineck (1923) reported that *C. hybrida* and *C. silvicola*, which burrow in sloping areas, build a semicircular lip above the entrance (apparently to deflect rain) and a pit below the entrance.

Shelford (1908) said that *C. limbalis* builds a chimneylike structure about 6 mm high at the entrance. Macnamara (1922) stated that the larvae of *C. tranquebarica* build a similar structure when necessary, as when an immovable obstruction is present. Hamilton (1925) said that an unidentified species from Colorado builds a chimney about 2.5 cm high in its early instars. Zikan (1929) showed a similar structure on a burrow of *Megacephala brasiliensis*. A second instar burrow of *C. fulgida* that I found in northern Kansas was situated among dead *Distichlis* stems; the larva had built a chimney about 0.5 cm high to elevate the entrance above these obstructions (other burrows of the same species had no such structure). This chimney-building habit is best developed in *C. willistoni*. Ortenburger and Bird (1933) first noticed this phenomenon in Oklahoma, but did not know which species is involved; I have studied it in Oklahoma and Kansas (in a new subspecies). In this species the larva always builds a chimney (called a turret by Ortenburger and Bird) relatively much higher than any other *Cicindela* known and adds two projections at the top, giving the apex a saddlelike appearance (Figs. 65-67). First instar turrets are usually 1-3 cm high; second and third instar turrets are 1.5-4 cm high (one second instar turret was 5.5 cm high). The apical projections have no special orientation. In the laboratory, larvae build shorter turrets and never add the projections. The function of these turrets is uncertain. They do not seem to serve for flood protection since they crumble in a heavy rain. Another possibility is to elevate the larva above the surface, which is the hottest part of the environment; however, when conditions become very hot and dry, the larvae usually plug their burrows and remain underground. A third possibility is that some insects that could serve as prey may be attracted to such projections as landing places.

At various times (after feeding, in unfavorable weather, before hibernation or estivation, before molting or pupation) the larva may close the burrow with a plug of soil. This is done by scooping a small amount of soil from the





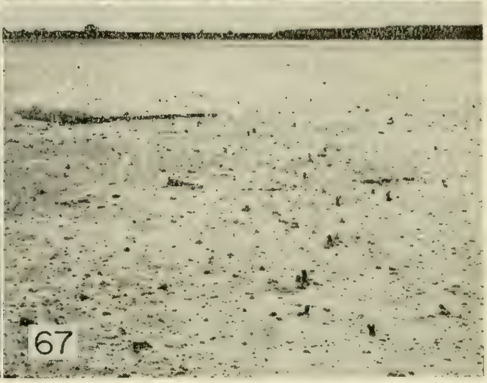


Fig. 65. Turret of third instar larva of *C. willistoni*, 2.5 mi. southwest of Plainview, Woods Co., Oklahoma. Fig. 66. Turret of second instar larva of *C. willistoni*, 11 mi. northeast of Hudson, Stafford Co., Kansas. Fig. 67. View of a number of turrets of larvae of *C. willistoni* on salt flat 2.5 mi. southwest of Plainview, Woods Co., Oklahoma; insect net is about 1 m long.

wall or bottom of the burrow onto the head and applying it to the entrance repeatedly. The burrow is unplugged in reverse fashion, the soil from the plug being plastered onto the walls. The thickness of the plug varies from less than one to several centimeters; it is thicker if the larva spends long periods underground (hibernation, pupation, etc.). I have noticed that the larvae in terraria often plugged their burrows temporarily soon after the soil was moistened. In nature this reaction probably saves their burrows from being flooded during rains.

Because the burrow diameter is nearly the same size as the head width, one can easily tell the instar of the occupant if one knows what species is involved. The latter reservation is necessary because the first instar burrow of a large species may be as large as the second or third instar burrow of a small species.

Food and feeding. After the burrow has been dug, the larva assumes a position at the entrance to lie in wait for food. The head and pronotum together form a circular lid or plug to the burrow and are usually colored so that the larva is very well camouflaged. Surprisingly, only one species of larva known from saline habitats, *C. togata*, has a light coloration of these parts of the body. However, some species, *C. nevadica* in this study, *C. silvicola* (Reineck, 1923), and *C. sexguttata*, accumulate a thin layer of soil on the pronotum and thus are even better camouflaged.

In maintaining its position at any point in the burrow, the larva uses its legs and abdomen. The front and hind legs are directed ventrad and the middle legs dorsad. The abdomen assumes a sigmoid position; the first five segments are bent ventrad, giving the larva a swayback appearance; the spines and large setae on the fifth abdominal tergum dig into one burrow wall; the rest of the abdomen is directed forward perpendicular to the axis of the burrow; and the spines on the tenth abdominal segment dig into the opposite burrow wall. Thus the larva is supported at eight points: the six legs and the fifth and tenth abdominal segments. To move down the burrow, the larva straightens its abdomen, flexes its legs, and if the burrow is vertical, falls with the aid of gravity (if the burrow is not vertical, the legs are used); to move up the burrow, the legs alone are used, although Shelford (1911) said that the abdomen assists also. Larvae are easily frightened and will drop down their burrows at the slightest footstep or movement of a human observer.

The larva usually lies in wait at the burrow entrance continually during favorable weather, by night as well as by day. Sometimes however, larvae close their burrows at night, and they frequently do so after feeding. If suitable prey alights or crawls over the burrow, it is very quickly seized by the larva's mandibles. A click is often heard when the prey is seized, apparently caused by the mandibles striking together. Wigglesworth (1929), in experiments on unidentified African species (probably of several genera), said that the larvae will not strike unless certain tactile setae on the back of the head and front of the pronotum are stimulated. Enock (1903), however, stated that the larva of *C. campestris* strikes when the prey is within 1.5 cm. He also gave a good description of how the larva strikes: the larva throws its body backward half out of the burrow; the median hooks of the fifth abdominal tergum dig into the edge of the burrow to anchor the larva. Friederichs (1931) noted the importance of vision in catching prey and said that the larva strikes in the above manner when the prey is between 3 and 6 cm away. Of course, if the prey should land very close to or directly on the head of the larva, it does not strike in the above manner, but simply snaps its mandibles shut on the prey. Probably vision is most important in the day and tactile senses at night for prey capture. The hooks of the fifth abdominal tergum, directed anteriad, serve to help prevent the larva from being pulled out of the burrow by strong prey.

Those species that build pits below the burrow entrance appear to use them as traps. Criddle (1910) and Shelford (1908) reported this for the larva of *C. formosa*; throwing small ants in the pit resulted in their immediate capture, according to Criddle.

The prey, if small enough, is usually dragged down the burrow to be eaten; if it is too large, it is held at the top of the burrow, but large prey items may be taken down the burrow after they have been partially eaten. A third instar larva of *C. circumpicta* that was observed in the laboratory sometimes quickly and sometimes slowly (in one case not for one hour) dragged the prey part way or all the way down the burrow; then it often turned around in the burrow before eating. Sometimes (in the laboratory) a larva, instead of eating the prey, would return to the entrance within a short time and lie in wait again. Two larvae of *C. willistoni* were thus "fed" repeatedly; one dragged 21 adult *Anagasta kuehniella* moths down its burrow, and the other 30, within one hour (three days later the first larva had thrown 13 moths out of its burrow, uneaten, and the other did the same with 15 moths three days after that; other uneaten moths were found when the burrows were dug up a month later after the larvae had died). Such behavior is probably not normal. In eating, the larva manipulates its prey slightly with its mouthparts. Wigglesworth (1929) said that larvae eject fluid (with a pH of 6.2-6.4 and containing trypsin) from the mid-intestine which predigests the prey; the larva then consumes the liquified tissues, straining out solid particles with setae on the labium. The hard cuticular portions of the prey are not eaten and are disposed of, either by tossing them out of the burrow or keeping them in the end of the burrow. The latter method has only been found to be used by *C. silvicola* (Reineck, 1923), *Megacephala brasiliensis* (Zikan, 1929), and *Amblychila cylindriformis* (Williams and Hungerford, 1914). Unacceptable prey is tossed away.

Larvae will eat nearly any small arthropod they can catch. Literature references indicate that food eaten in nature includes caterpillars and other insect larvae, butterflies, moths, flies, beetles, dragonflies, ants, spiders, centipedes, and land crustaceans. In captivity, larvae have been fed houseflies, ants, sowbugs, small beetles, decapitated woodboring larvae, ant pupae, thysanurans, caterpillars, small pieces of raw meat, and apple (it is unlikely that apple was eaten). Criddle (1910) said that larvae of *C. formosa* do not accept Hemiptera. I have only once found a larva eating in nature, a first instar larva of *C. willistoni* that had a salticid spider at the top of its turret. Dr. F. E. Kurczewski (personal commun.) has seen larvae of an unidentified species eat a wasp, *Tachysphex terminatus*. In the laboratory I have fed larvae small spiders and phalangids (a large phalangid was refused), mayflies, nymphal short- and longhorned grasshoppers, nymphal cockroaches (*Supella supellectilium*), mirids (*Adelphocoris rapidus* and others), nabids, cicadellids (nymphs and adults), an immature fulgorid, aphids, chrysopids, a small cantharid, trichopterans, various caterpillars (including arctiids, geometrids, and a noctuid), small adult moths (including *Anagasta kuehniella*), small adult flies (including a culicid, a syrphid, a bombyliid, a trypetid, a calliphorid, and other muscoid species), and ants. An immature cercopid was not readily accepted. Silphid, coccinellid, and chrysomelid larvae were rejected (one coccinellid larva was manipulated by the larva's mouth-parts for 10-15 seconds, then forcibly flipped out of the burrow unharmed). Sawfly larvae (Tenthredinidae ?) were sometimes refused and sometimes eaten. A small bee was refused by one larva but accepted by another. Goldsmith (1916), Macnamara (1922), Reineck (1923), Schaupp (1879b), and Shelford (1908, 1911) mention that larvae may eat each other in captivity. Some authors attribute cannibalism to crowding and others to hunger. I have noted cannibalism once; a beheaded larva was found outside its burrow in a jar that contained three larvae. Dr. F. E. Kurczewski (personal commun.) has seen on three occasions an unidentified species of larva in Groton, Tompkins County, New York, eating adult *C. formosa*, starting at the abdomen. As will be mentioned later, I once found a *C. circumpicta* with its abdomen missing. We may thus conclude that nearly all small arthropods are acceptable as food to larval *Cicindela*. The time since the last meal probably also affects the acceptability of food, but has not been investigated.

Macnamara (1922) was surprised to find how seldom larvae catch prey in nature; in over ten hours of watching a group of *C. tranquebarica* larvae, he only saw one small ant eaten. He also said that the larvae throw their semi liquid excrement away from the burrow.

The time interval between meals depends on the individual, the instar, the size of the meal, and probably also on the species and temperature. Some larvae in the laboratory ate *Anagasta kuehniella* moths about every other day, while others ate very irregularly and often fasted for a number of weeks. The rough treatment of being caught and transported and the artificial conditions in the laboratory apparently made some larvae refuse to come to the tops of their burrows for food, with the result that they starved to death. In nature, of course, nothing is eaten during estivation or hibernation.

Molting and stadia. First instar larvae only need one meal (if it is large enough) to store enough energy to molt; second and third instar larvae need several meals. As mentioned above, the larva usually closes its burrow while it molts. Shelford (1908) stated that the larvae he studied take about five to seven days to molt; i.e., the burrow is closed that long (as far as is known, no one has seen the actual molting process). Zikan (1929) found that some tropical genera have five instars and close their burrows for two to four weeks during molts. Huie (1915) reported that *C. campestris* larvae closed their burrows about ten days while molting at the start of the second instar. I have

TABLE 3. Length of stadia in days of larvae reared in the laboratory. Numbers between dots are numbers of days spent between the two events in the respective columns; numbers in parentheses are number of *Anagasta kuehniella* adults (A) or larvae (L) eaten.

Species	First Instar burrow open		First Instar burrow closed		Second Instar burrow open		Second Instar burrow closed		Third Instar burrow open		Third Instar burrow closed
C. circumpicta	●	12	●	102	●	34	●	105	●		
						8(A)					
C. duodecimguttata									●	47	●
C. nevadica					●	—	26	—	●		
					●	—	148	—	●		
C. togata			●	22	●	29	●	14	●	243	●
						(8A)				(14A)	
					●	68	●	72	●	91	●
						(5A)				(15A, 1L)	
					●	110	●	54	●	62	●
						(7L)				(13A)	
										217	
									●	31	●
										(4A)	
					●	54	●	37	●	52	●
						(7A, 2L)				(9A)	
	●	—	99	—	●	—	39	—	●		
					●	—	114	—	●		
C. willistoni	●	—	19	—	●	1?	●	12	—	193	●
										(13A)	
			●	9	●	17	●				
						(9A)					
						118					
					●	341	●				
						(40A)					
			●	8	●	27	●				
						(5A)					

found that a larva of *C. duodecimguttata* in the laboratory closed its burrow four days to molt from first to second instar, while a *C. willistoni* took seven days to make the same molt (after eating one *Anagasta kuehniella* three days before closing its burrow). These seem to be minimal times; other larvae closed their burrows for many weeks or months, then appeared as the next instar. The enlargement of the burrow to fit the new instar occurs after molting.

The interval between molts (stadium) varies with the individual, the species, the instar, abundance of food, amount of favorable weather, and temperature. Shelford (1908) stated that the first instar larva of *C. limbalis* molts about three to four weeks after hatching; the other stadia are much more variable, the second being about five weeks and the third about ten to eleven months under favorable conditions. Huie (1915) said that the first stadium of *C. campestris* is about six weeks. Zikan (1929) found that the stadia lasted from one to four months, the first being the shortest. Stadium lengths and molting intervals found in this study are shown in Table 3. As can be seen, there is much individual variation, much is probably due to the artificial laboratory conditions. There seems to be much less variation in the amount of food consumed in a stadium than in the length of stadia. The number of moths eaten in normal second stadia ranged from 5-9, and 9-15 for third stadia; the first instar probably can molt after eating one moth. The average weight of an *Anagasta kuehniella* adult is about 0.01 g; thus the amount of whole moths needed for the stadia is: first stadium, 0.01 g; second stadium, 0.05-0.09 g; third stadium, 0.09-0.15 g. Because of the individual variation and the small number of larvae reared in this study, few definite conclusions can be drawn about the lengths of stadia. For *C. togata,* the minimum time for the second stadium under laboratory conditions is about four to five weeks. As will be seen later, hibernation and estivation greatly lengthen the stadia in which they occur.

Activity. Field observations indicate that some larvae of most species are active throughout the warm months (in Kansas, from about March through October). This is partly because of the overlap of generations and long life cycle of cicindelids. If conditions become severe (high temperature or drying out of the soil), estivation usually occurs. As mentioned above, larvae are active day and night, but probably not on cold nights.

Those species that live so near the margins of saline habitats that their burrows are near vegetation or on the side of a bank or hummock probably are able to be active for a longer time than species living on bare flats; the vegetation probably reduces the extremes of temperature and temperature fluctuation found on bare flats. However, there is the possibility that larvae of bare flats compensate for this by digging deeper burrows.

Microhabitats. Many authors have noted that the larvae of one species or another occur only in limited or characteristic areas. Shelford (1911) made a detailed study of *C. limbalis*, *C. tranquebarica*, and *C. sexguttata*, and found that the larvae of these species are found in quite restricted areas characterized by vegetation, exposure, slope, and kind and moisture of soil. In laboratory experiments, he found that the adults choose optimum microhabitats for oviposition (see more complete discussion under the adult). Microhabitats of larvae in this study are shown in Table 4.

Table 4. Microhabitats in which larvae have been found. The greater the number of X's the more frequent the occurrence of larvae.

Species	Near water, sand bar	Sloping bank, creek bank	Moist bare salt flats	Dry bare salt flats	Small flats, near margin	Near hummocks, among vegetation
C. circumpicta		XXX			XX	XXX
C. duodecimguttata	XX	XXX				
*C. fulgida**		XX			XX	XXX
C. nevadica		X			XX	XXX
C. togata		X	XXX	XX	XX	XX
C. willistoni			XXX	XX		

* Few larvae have been collected of this species.

As noted above, larvae usually dig their burrows where their eggs were oviposited; however, a number of workers have found that the larvae of some species will leave their burrows if conditions are unsuitable. Shelford (1908, 1911) stated that the larvae of *C. hirticollis* and *C. repanda* often leave their burrows if the soil becomes too dry or too wet; under extreme conditions, such as flooding of the habitat, a small percentage of larvae of the other species he studied left their burrows. Montgomery and Montgomery (1930) also noted larvae of *C. hirticollis* leaving their burrows, and Hefley (1937) saw larvae of *C. cuprascens* moving to a cooler, moister place.

The question of how species of fluvial habitats, whose larvae inhabit sand bars and stream banks, survive flooding is intriguing. Criddle (1907) thought that both larvae and adults of *C. duodecimguttata* must often die in hibernation when their habitat is flooded. Hamilton (1885) noted that hibernating adult *C. repanda* survived flooding for seven days. I have seen active larvae and swarms of adults in areas that had been recently flooded, so cicindelids most certainly do survive flooding. Possibly air trapped in their closed burrows is instrumental in their survival. Floods that cause much erosion probably wash out and kill many beetles.

Larvae can tolerate a certain amount of disturbance of their habitat, such as cattle walking and disfiguring the soil or plowing by man, but cicindelids are generally absent from areas where such disturbance is frequent or prolonged.

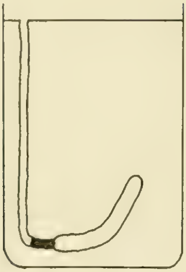
Predators and parasites. Predators of larvae are few; Grandi (1951) stated that histerid beetles of the genus *Saprinus* penetrate larval burrows and eat the occupants; Zikan (1929) said that birds occasionally eat larvae, and that ants *(Solenopsis geminata)* frequently dig into the larval burrow, sting the larva, and eat it; Shelford (1911) reported that ants may overcome a *C. limbalis* larva, and after chewing off its antennae and tarsi, drag it from the burrow. No evidence of predation on larvae was seen in this study.

A number of larval parasites are known. Reineck (1923) reported that *C. silvicola* larvae are occasionally found dead and covered by a moldlike substance; however, he did not mention that the larvae might have died from other causes and their dead bodies later attacked by fungi. Shelford (1913a) studied the life history of a bombyliid fly, *Anthrax analis*, which he found parasitizing *C. scutellaris* and *C. hirticollis*. The adult fly oviposits in larval burrows; the fly larvae attach to the thorax or abdomen of the cicindelid larva and feed from the outside. After the cicindelid larva has built its pupal cell (see next section), the last instar fly larva pupates. The fly pupa digs its way to the surface and the adult emerges. Shelford also said that the larvae of *C. limbalis* were parasitized by a larva somewhat different from *Anthrax analis*. Hamilton (1925) stated that four larvae (out of 34 collected) of *C. obsoleta* (?) were parasitized by a total of seven dipterous larvae, which he assumed to be *Anthrax analis*. Frick (1957) reported that he saw a small black bombyliid (not collected) oviposit in three larval burrows of either *C. haemorrhagica* or *C. pusilla*; the burrows were soon closed by blowing sand, and in a few weeks no larvae could be found. Williams (1916) found some larvae of *C. punctulata* (?) parasitized by orange maggots, probably *Anthrax*. Batra (1965) saw *Anthrax analis* apparently ovipositing in burrows of cicindelid larvae. James K. Lawton *(in litt.)* has found larvae of *C. tranquebarica* in Wisconsin parasitized by *Anthrax analis*; adults were seen ovipositing one to three times in larval burrows. Dr. F. E. Kurczewski (personal commun.) has seen *Anthrax albofasciatus* ovipositing in *Cicindela* larval burrows in New York. I have often seen adults of *Anthrax analis* in saline habitats and once saw one oviposit repeatedly in two burrows of second instar *C. togata* (?) before being collected. The fly lands beside a burrow, stands high on its legs, and bends the tip of its abdomen forward, flipping eggs at the entrance. I have found no parasites on any larvae that I have collected throughout the central United States.

Criddle (1919) stated that the chalcid wasp, *Tetrastichus microrhopalae* (Eulophidae), was reared from *C. limbalis* larvae. Williams (1928) reported that two species of tiphiid wasps of the genus *Pterombrus* (misspelled "*Pterombus*") parasitize larvae of *Cicindela* sp. and *Megacephala affinis* in Brazil. A number of species of the tiphiid genus *Methocha* have been found to parasitize cicindelid larvae: *M. ichneumonides* in Europe (Bouwman, 1909; Champion and Champion, 1914; Champion, 1915; Pagden, 1925; and others), *M. striatella* and *M. punctata* in the Philippines (Williams, 1919), *M. japonica* and *M. yasumatsui* in Japan (Iwata, 1936), *M.* sp. in Brazil (Zikan, 1929), *M. californicus* in California (Bridwell, 1912; Burdick and Wasbauer, 1959), and *M. stygia* in Massachusetts (Williams, 1916) and Wisconsin (James K. Lawton, *in litt.*). The antlike female wasp approaches a burrow with the larva lying in wait at the entrance and induces the larva to seize it (in other cases the wasp avoids the mandibles of the larva). Then the wasp curls its abdomen under the heavily sclerotized head and stings the larva in the tender, membranous neck region, paralyzing it. After secondary stingings, the wasp lays an egg on the venter of the thorax or abdomen. Then the burrow is closed partially or level with the surface by the wasp. The wasp larva feeds from the outside and may change positions. Pupation occurs off the remains of the host. No parasitism by Hymenoptera was noted in saline habitats; however, a *Pterombrus rufiventris* was collected on salt flats in northern Kansas. The life cycle of this species is unknown.

The pupal cell. Before pupation the third instar larva closes its burrow (normally) and digs a chamber for pupation, the pupal cell. The diameter of the pupal cell is about twice that of the larval burrow. It may simply be an enlargement of the larval burrow or adjoin the larval burrow directly (*C. campestris*, Enock, 1903; *C. limbalis*, *C. lepida*, *C. punctulata*, Shelford, 1908). In other species, a tunnel the same diameter as the larval burrow and branching off the latter is built between the pupal cell and the larval burrow (*C. limbata*, Criddle, 1910; *C. scutellaris*, Shelford, 1908). The soil from these new cavities is used to plug much of the larval burrow. The walls of the pupal cell are made smooth by the larva with the mandibles and ventral side of the head. The shape of the pupal cell varies in different species; in some it is only about twice as long as wide and oval; in others it is very elongate and slightly bowed. There is some intraspecific variation in the shape and position of the pupal cell relative to the larval burrow. The pupal cell is built relatively close to the surface, often as close as 2.5 cm. Shelford (1908) found in experiments that the depth of the pupal cell is influenced by soil temperature, being greater the warmer the soil. Some typical pupal cells that I found in laboratory-reared individuals are shown in Figures 68-71.

THE PUPA. Having completed construction of the pupal cell, the larva becomes quiescent, head up, with the thorax and abdominal hump resting against the bottom or side of the cell. At the end of one to three weeks, it is not able to move its legs. The abdomen gradually thickens and turns a translucent cream color, indicating internal changes. The tubercles of the first five abdominal segments of the pupa (see below) can be seen through the larval skin folded toward the midline. A few days after these changes, the larval cuticle splits along the frontal suture of the head and the dorsal thoracic midline. Contractions of the ventral muscles flex the body slightly, and the head is gradually withdrawn. The abdomen is freed by later movements. Ecdysis is accomplished in only a few minutes. Just after emergence, the pupa is only slightly shorter than the larva, but it soon contracts to its normal size. The above events have not been seen personally and have been taken from Shelford (1908) and Enock (1903). However, one larva of *C. circumpicta* became quiescent after digging the pupal cell the previous two days;



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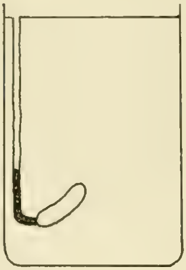

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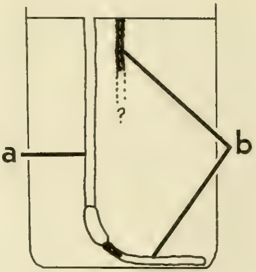

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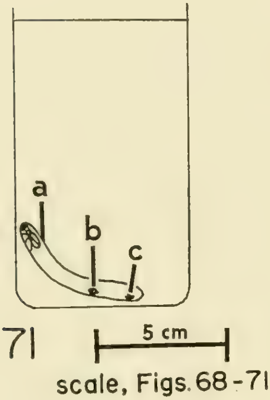

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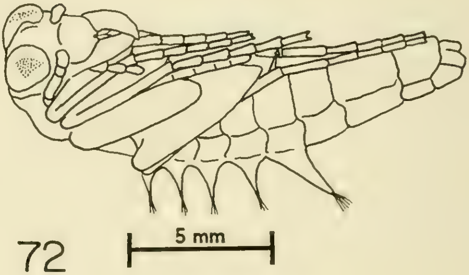

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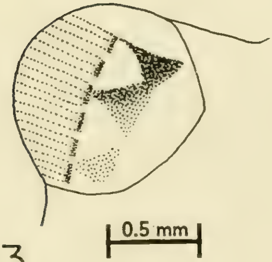

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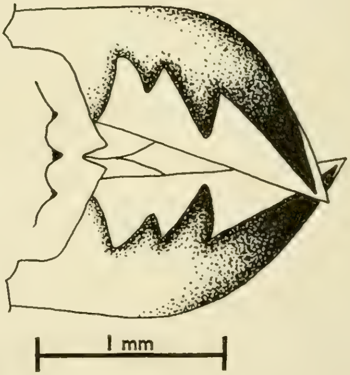

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Figs. 68-69. Pupal cells and larval burrows (partly plugged) of *C. circumpicta*, from 1 mi. northwest of Fredonia, Wilson Co., Kansas, shown in laboratory rearing jars. Fig. 70. Pupal cell, adult escape burrow (a), and portions of larval burrow (b), partly plugged, of *C. togata*, from 3 mi. west, 2 mi. south of Barnard, Lincoln Co., Kansas, shown in laboratory rearing jar. Fig. 71. Pupal cell with newly emerged adult (a), pupal skin (b), and larval skin (c) of *C. nevadica*, from 11 mi. northeast of Hudson, Stafford Co., Kansas, shown in laboratory rearing jar. Figs. 72-74, *C. cimcumpicta* pupa; Fig. 72, newly emerged pupa, from 11 mi. northeast of Hudson, Stafford Co., Kansas, ventrolateral aspect; Fig. 73, right eye, caudal aspect; Fig. 74, labrum and mandibles of pupa, from 1 mi. northwest of Fredonia, Wilson Co., Kansas, ventral aspect; pupa is about 18 days old.

the period of quiescence lasted 28 days. A freshly emerged pupa of another individual of the same species was dug up 16 days after the larva was last seen.

The newly emerged pupa of *C. circumpicta* (Fig. 72) is creamy white; the thoracic region is darker yellow, and part of the eyes contains light tan pigment arranged in columns (Fig. 73). The first four abdominal segments bear paired dorsal tubercles, each with an apical ring of setae. Those of the fifth segment are larger. The setae and tubercles function to hold the pupa off the substrate. Shelford (1908) gave a brief summary of pupal color changes in *C. purpurea*: in about ten days the eyes have become completely dark brown; about two days after that, the tips of the mandibles and mandibular teeth begin to darken; the darkening of the mandibles is complete in one to two days; about 13 days after pupation, the tarsal claws begin to darken; and 14 to 15 days after pupation, the proximal portion of the tibiae and the outer margins of the trochanters begin to darken. In 1917, Shelford gave a slightly more detailed schedule for *C. tranquebarica*: initial stages are about the same as for *C. purpurea*; the darkening of the tibiae, which spreads from proximal to distal parts, takes two to three days; about the time that this occurs, the middle of the folded adult hind wings (appear as the tips of the pupal wings) begin to darken; color centers on the last two abdominal segments may develop just before emergence of the adult.

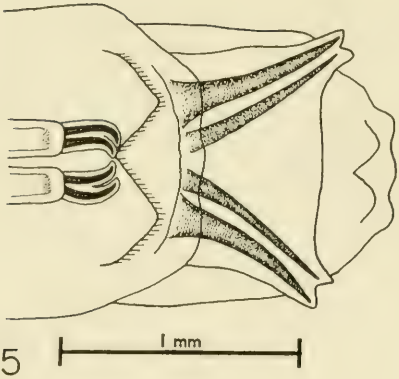
Four pupae of *C. circumpicta*, kept in Stender dishes, were observed during all or part of their development. In the following schedule, the numbers indicate the approximate number of days after emergence:

0-12 or 16: the eye pigment gradually becomes diffused and darker reddish brown until the eyes are uniformly dark brown.

14-18: tips of the labral and mandibular teeth and tarsal claws begin to turn brown (the latter two usually start slightly before the labrum), a process that takes about 1-1.5 days (Fig. 74); soon after this, the apical tibial spines also begin to turn brown.

16-19: a metallic purplish and green iridescence begins to appear on the frons, first antennal segment, and tibiae, later spreading over the head and legs.

17-19: parts of the genitalia begin to turn brown (gonapophyses in ♀ [Fig. 75], aedeagus in ♂), the posterior margin of the eighth abdominal sternum (of ♀) begins to turn brown, the proximal ends of the tibiae and the margins of the trochanters become light brown, and the tips of the pupal hind wings (=middle of folded adult wings) turn light gray; soon after this, spots of light brown appear on the labrum at the bases of the submarginal setae, the apices of the tarsal segments and the tips of the terminal maxillary palp segments become light brown; the terminal few segments of the antennae become light gray, the laciniae of the maxillae become brown, and the clypeal region turns light brown. By now, light brown areas have



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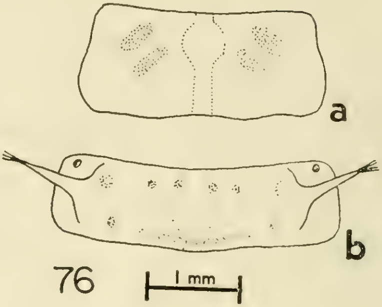

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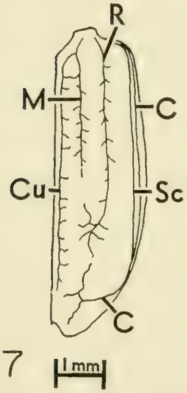

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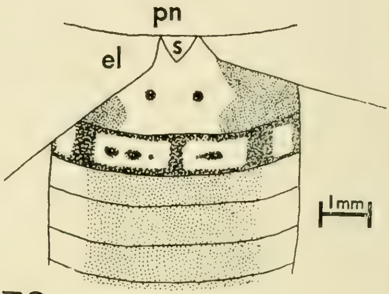

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FIGS. 75-76, *C. circumpicta* pupa; FIG. 75, Eighth, ninth, and tenth abdominal segments and apices of hind tarsi of female, ventral aspect; pupa is about 19 days old; FIG. 76, metathoracic (a) and second abdominal (b) terga of same, dorsal aspect; the middorsal position of the heart is shown by dotted lines. FIGS. 77-78, *C. circumpicta* adult, from 11 mi. northeast of Hudson, Stafford Co., Kansas; FIG. 77, venation of right elytron (recently emerged), dorsal aspect; C=costa, Sc=subcosta, R=radius, M=media, Cu=cubitus; FIG. 78, mesonotum, metanotum and first three abdominal terga, 15 hours after emergence, dorsal aspect; pn=pronotum, el=elytron, s=scutellum.

appeared on the dorsum of the thorax and abdomen (Fig. 76); the beating heart can easily be seen through the dorsal cuticle, its rate being somewhat variable, with occasional stops, and averaging about 37 beats per minute. The gray of the pupal hind wings spreads to about half their visible surface and becomes darker; about half the tibiae become brown, and the tips of the terminal maxillary palpal segments become dark brown; also the tarsal tips may begin to twitch at or before this point. The gray of the antennae spreads proximad; the pupal skin begins to shrivel, and the dorsal abdominal tubercles become soft.

18-21: the tibiae and tarsi are completely brown (the proximal parts of the tibiae are darkest), and the proximal ends of the femora begin to turn brown. The lateral and posterior margins of the labrum begin to turn brown, the proximal halves of the pupal hind wings begin to turn light gray (the distal halves are very dark gray), the genitalia become darker, and the last three abdominal sternal margins (♀) are light brown. The rest of the maxillary palpal segments become light brown, the bases of the first antennal segments begin to turn brown, the terminal antennal segments are dark gray, and the distal tips of the first, second, and third segments are light brown; the trochanters are dark brown, the distal ends of the coxae and margins of the coxal cavities are brown, and iridescent reflections are visible on all parts of the head and eyes. Movements of the legs, maxillary palps, mandibles, and genitalia may be seen within the pupal skin, and the abdomen may swell and contract slightly. An hour or so later, the movements become more extensive: the head and prothorax are flexed backward; the whole body may be moved slightly (straightened); the mandibles, labrum, maxillary palps, genitalia, and legs are flexed; abdominal movements continue; finally, the legs and maxillary palps are moved freely. The adult may emerge at this point or such movements may continue for several hours. After a flexing of the head and prothorax, the pupal skin is apparently broken dorsally, because several seconds later air bubbles can be seen in the fluid beneath the pupal skin, and the nonbrown portions of the labrum and mandibles, which were translucent, quickly become opaque creamy white. Movements of the abdomen, head, thorax, and appendages assist in extricating the adult from the pupal skin. After about an hour, the head, antennae, front and middle legs, and entire dorsum are free. The body setae are wet and matted. After about two hours the adult has emerged completely. As implied above, the time spent in the pupal stage varies from 18 to 21 or 22 days at a temperature of 24.5°C.

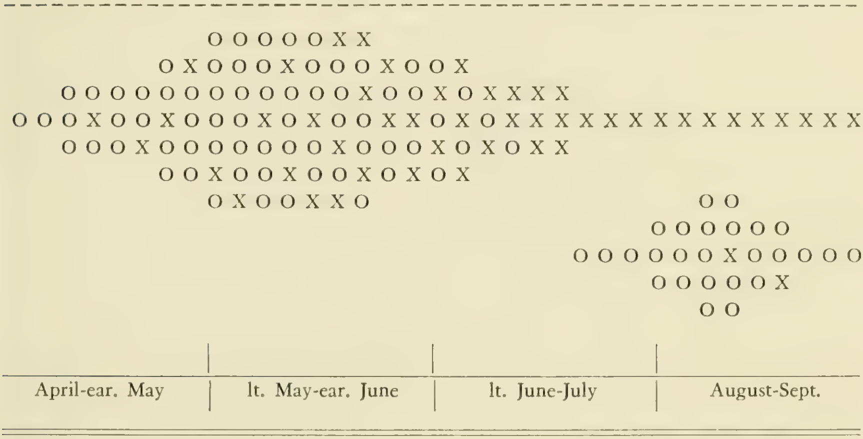
The Adult—*Post Emergence Changes.* Following emergence, hardening and darkening of the adult cuticle is completed. Shelford (1917) described the process in detail for *C. tranquebarica* and less completely for several other species. At the time of emergence, the stage of sclerotization of *C. circumpicta* is more advanced than in *C. tranquebarica* (see description of pupa just before emergence). The newly emerged adult is creamy white except for the above noted parts. The elytra are expanded before the pupal skin is completely off. About 1.5 hours after emergence, the elytral pattern becomes visible because their future pigmented parts have a faint green metallic color. The tracheae of the elytra are easily visible at this time; the typical venation is shown in Figure 77. About 1.5 to 2 hours after emergence, the hind wings are fully expanded and begin to change from translucent to transparent; the veins begin to darken. About 3 to 4 hours after emergence, the distal wing veins are noticeably darker, and about 4 hours after emergence, the hind wings are folded. About 15 hours after emergence the head, prothorax, and femora are light brown, and the elytra are very light brown except where the white pattern will be. The meso- and metanota are creamy white with a few gray spots, and the abdominal dorsum is creamy laterally and dark gray mesally (Fig. 78). The antennal scape and pedicel are brown, the distal ends of the third and fourth antennal segments are brown, and the sixth to eleventh segments are dark gray. In about 3 to 4 hours, the head and prothorax are dark brown and the elytra are brown except the future white pattern, which is translucent creamy white. At about this time, if the individual is a female, the terminal abdominal segments (eighth, ninth, and tenth) begin to retract, a process that is completed about 40 hours after emergence. About 24 hours after emergence, the elytral pattern begins to become more opaque white. About 40 hours after emergence, the beetle can support its own weight and stand. About 68 hours after emergence, the venter of the abdomen is dark, and the antennae, which were held close to the body over the back, are held out in the normal position perpendicular to the long axis of the body. The beetle now becomes quite active, and in nature, adults probably begin digging their way out of the soil at this stage. In captivity, beetles will accept food four to seven days after emergence. About six days after emergence, the elytral pattern becomes opaque white. In the field, adults have been collected with the elytra soft and the pattern still opaque, supporting the conclusion that they dig out of the soil about three days after emergence.

Besides the above changes, a series of color changes, begun in the pupal stage, occurs before the final adult color is acquired. Shelford (1917) studied this in detail, and Huie (1915) noted that on the third day after emergence, *C. campestris* is bluer than when more mature. In *C. circumpicta*, a number of color forms occur, most individuals being either reddish, green, or blue. In the early stages, all individuals show about the same colors: green, blue, and purple on the head, thorax, proximal antennal segments, and legs in the pupal stage and early post-emergence period. In a future green individual, the changes are as follows: from about 4 to 17 hours after emergence, the elytra become almost completely purplish; about 18 to 20 hours after emergence, the head and pronotum, which were purplish, have become brassy green, and the elytra have become purplish and blue; about 40 hours after emergence, the blue of the elytra has increased, a process that continues for over a day; about 70 hours after emergence, the elytra begin to acquire a turquoise color; and about four days later there is more green than blue in the elytral color, but the margins still have a purplish tinge; there is little color change after this. An individual that finally had blue elytra and a green-blue head and pronotum, first had purple-blue elytra and a blue-green

Table 5. Percentage of adult *C. f. fulgida* in two color classes (dorsal color) collected at four times of the year in the central United States, and sample size.

Time of coll.	% Bright red	% Purplish red	N
April-early May	72.5	27.5	40
Late May-early June	59.0	41.0	464
Late June-July	20.5	79.5	39
August-September	50.0	50.0	128

Probable scheme of color change in *C. f. fulgida.* The width of the band indicates the abundance of specimens; O=bright red, X=purplish red.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April-ear. May
lt. May-ear. June
lt. June-July
August-Sept.

head and pronotum. An individual that finally had dark cupreous elytra and a brownish head and pronotum was mostly green and cupreous three hours after emergence; the green then increased for about a day, then a reddish wine predominated for about two days before the final color appeared.

As Shelford (1917) noted, individuals of some species continue to change color long after emergence, sometimes until death. I have found that this occurs in *C. fulgida*, at least in its southern subspecies, *C. f. fulgida.* I noticed that most adults collected from northern Kansas in September 1963, and kept in the laboratory over winter were dark purplish red (dorsally) in the spring instead of bright red as they were when captured. When about 270 specimens in my collection and 400 in the Snow Entomological Museum were categorized according to color and time of year collected (Table 5), a trend was noted for most specimens collected in the spring to be bright red and late summer specimens to be dark. A chi square test of independence in a 4 x 2 table was performed on the original data (not %), with the null hypothesis (H_o) being that the time of collection and color are independent. A highly significant X^2 of 27.7 was obtained, rejecting the H_o and indicating that the color is dependent on the time of collection. Three chi square tests with one degree of freedom were then performed: no significant difference was found between the April-early May and the May-early June groups ($X^2=2.9$); the late June-July and August-September groups were significantly different ($X^2=10.6$); the two early groups combined and the late June-July groups were significantly different ($X^2=21.9$). The bottom of Table 5 shows qualitatively a possible scheme for such data. As will be discussed in more detail later, *C. fulgida* is called "double brooded"; that is, adults emerge from the pupae in the late summer and fall, hibernate, emerge the next spring, and gradually die out in the summer. Freshly emerged individuals are bright red, gradually becoming darker.

THE ADULT—*Mating*. Many species begin to reproduce soon after emergence as adults, but, as will be discussed later, others hibernate as adults and do not become sexually mature until the spring after they emerge. When sexually mature, and if the weather is suitable, the adults do little else than eat and reproduce. Mating has been observed by a number of workers in the past and seems to be similar in all the genera (Mitchell, 1902, for *Megacephala carolina* and *C. ocellata*;[3] Shelford, 1908, for *C. purpurea*; Moore, 1906, for *C. repanda*; Lengerken, 1916, 1929, for *C. hybrida* and *C. martima*; Goldsmith, 1916, for *C. punctulata*; Fackler, 1918, for *C. cuprascens*, *C. hirticollis*, and *C. repanda*; Zikan, 1929, for *Cicindela*, *Prepusa*, *Euprosopus*, *Iresia*, *Oxychila*, *Odontochila*, and *Megacephala*; Lesne, 1921, for *C. silvicola*; and Pratt, 1939, for *Omus*). I have closely observed mating in the laboratory in *C. circumpicta*, *C. fulgida*, *C. nevadica*, and *C. togata*; and mating pairs of many other species were frequently seen in the field.

The males "take the initiative" and usually approach a female in short runs. When several centimeters away, the male makes a final quick dash and leaps on the dorsum of the female, grasping her between the prothorax and elytra with his mandibles, and frequently around her abdomen with his first and sometimes second pair of legs. Males have a dense brush of setae on the venters of the first four front tarsal segments that are apparently an adaptation for grasping the female. The male supports himself with the last and sometimes second and first pairs of legs (Fig. 79). Males are quite aggressive and have been seen trying to mount other males (specimens pinned on the same pin as "mating pairs" have been seen in museum collections that consisted of two males of the same or different species) or mounted pairs. The female may unseat the male as soon as he mounts and drive him away. If not, the two beetles may remain in the mounted position for some time before or after copulation (a half hour or more), and often the female "goes about her business" of eating, drinking, or ovipositing with a male riding along

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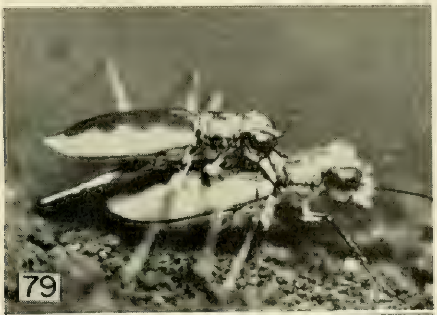
[3] The species which students of American cicindelids have been calling *C. flavopunctata* Chev. should be called *C. ocellata* Klug because the former name is a junior homonym (Schilder, 1953a).



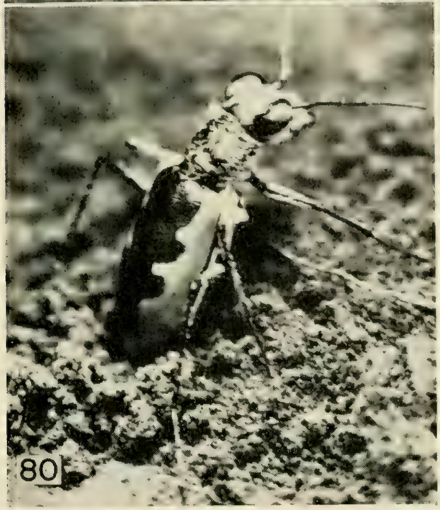


Fig. 79. Mounted pair of *C. togata*, from 3 mi. west, 2 mi. south of Barnard, Lincoln Co., Kansas. Note male's use of mandibles in grasping female. Fig. 80. Ovipositing *C. togata*, from same locality.

(thus, because specimens collected in the field were mounted, this does not mean that they were actually mating). Eventually, the male everts his aedeagus, which normally is retracted within the abdomen, and brings it into a ventral position pointing forward, attempting to insert it into the female's genital opening. The female may make this difficult by turning the end of the abdomen down and may even drive the male away. If the male is successful, the aedeagus is inserted one or several times for one to several minutes each. At this time, the pair may touch and quiver their antennae. Lengerken (1929) said that the male strokes the female's elytra with the palpi of the mouthparts, but I have not seen this. Following couplation, the male may remain mounted or be driven off by the female. Males and females may mate repeatedly with the same or different partners.

The literature mentions mating in the daytime only, and Lengerken (1929) said that it only occurs during hot sunshine; however, I have seen a number of mounted pairs of *C. circumpicta* near Roswell, New Mexico, after dark in the early evening (the soil was still warm from the day). Shelford (1911) mentioned seeing *C. tranquebarica* mating and ovipositing in the laboratory on damp, cloudy days.

THE ADULT—*Oviposition.* Oviposition has occasionally been seen in nature. Ponselle (1900) mentioned it for *C. flexuosa*; Mitchell (1902) saw it in *Megacephala carolina* and *C. ocellata*; Moore (1906) twice saw *C. repanda* ovipositing; Shelford (1908) reported on *C. purpurea*; Huie (1915) noted that *C. campestris* fills the oviposition hole and may eat its own egg if disturbed during oviposition; Goldsmith (1916) said that *C. punctulata* may oviposit in cracks if the soil is hard; Fackler (1918) briefly commented on *C. repanda*; Lesne (1921) reported on *C. silvicola*; Lengerken (1929) mentioned that eggs are apparently laid singly in the soil; Zikan (1929) said that all the cicindelids he observed close their oviposition holes with material from a second hole made at the same site but slanting obliquely.

I have observed oviposition in the laboratory in *C. circumpicta* and *C. togata.* The ovipositor consists of the eversible terminal abdominal segments (eighth, ninth, and tenth) and the sclerotized gonapaphyses of the eighth and ninth segments, and has been morphologically studied by Shelford (1908), Tanner (1927), and Zikan (1929). In seeking an oviposition site, a female *C. togata* was seen touching her antennae to the soil and occasionally biting the soil with her mandibles. Occasionally, she dug for a short time with her ovipositor. Females often dig holes into which no egg is laid. These have been called "exploratory" or "test" holes, in the literature. When a suitable site has been found, the female digs a true oviposition hole. In digging, the ovipositor is everted and the body is inclined at a steep angle by the front and middle legs (steeper in *C. togata* than in *C. circumpicta*). The hind legs are spread wide for support (Fig. 80). The gonapophyses are the primary digging tools, and the abdomen makes assisting thrusting motions. Sometimes some soil is removed from the hole by an upward motion of the whole body. The oviposition holes takes about five to ten minutes to dig and is from 0.5 to 1 cm deep. The female then remains quiet for several seconds while the egg is laid. Then the hole is usually filled, apparently sometimes with soil from an oblique hole at the same site, as reported by Zikan (1929), and also using the loose soil around the hole that was thrown out in digging. The soil is tamped with the end of the ovipositor, the whole body assisting in the motions, and finally the soil is raked with the gonapophyses, leaving little or no trace of its having been disturbed. The filling of the hole takes one or two minutes; the entire oviposition process usually takes eight to twelve minutes. Occasionally, *C. togata* have been seen not to fill the oviposition hole, and Shelford (1908) said that *C. purpurea* does not close its holes. This would seem to be very harmful to the egg by permitting desiccation. One egg is laid in each hole. I have only once seen a cicindelid oviposit in nature, a *C. circumpicta* near a saline pool near Roswell, New Mexico, on a hot, sunny day.

Shelford (1908) reported watching a *C. purpurea* lay about 50 eggs, and was uncertain as to whether more might be laid. This is the only known estimate of fecundity.

Shelford (1911) did interesting experiments on the selection of the oviposition site, placing adults in cages containing different types of soil and different degrees of slope and moisture. He found that *C. limbalis* chooses only clayey soil and prefers steep slopes; *C. tranquebarica* oviposits in many kinds of soil, but prefers sandy, moist soils; *C. sexguttata* prefers sand with a small amount of humus and usually oviposits near or under twigs or leaves. He also noted that oviposition sites are different from or more restricted than the habitats in which the adults hunt for food. Thus it seems that the adults select optimal microhabitats for the larvae.

The Adult—*Food and feeding.* There have been many notes in the literature concerning the food of adult cicindelids; those for the genus *Cicindela* are summarized in Table 6. In addition, past workers have fed the following to adults in captivity: decapitated woodboring beetle larvae, mealworms (*Tenebrio* larvae), caterpillars, a tipulid fly, a large tabanid fly, calliphorid larvae and adults, freshly killed house flies, and ants. Arthropods that I have seen eaten or attacked by *Cicindela* in the field and in the laboratory are listed in Table 7. From these lists, one may conclude that adults of *Cicindela* eat nearly any arthropod that they can subdue and which occurs in their microhabitat. Occasionally, a beetle will reject an insect that possibly may possess distasteful chemicals, but at other times such insects are eaten. Probably the degree of hunger of the predator affects the acceptability of distasteful prey.

Balduf (1925) observed a *C. punctulata* catch and eat nine large nymphs and one adult chinch bug, *Blissus leucopterus*, in 26 minutes. The beetle saw the bugs from 5 to 8 cm away (in all cases they were moving), and after catching them in its mandibles, struck them against the ground several times in rapid succession before eating them. The beetle returned to a certain elevated spot to eat; the exoskelton of the prey was discarded in the form of a small pellet. Lesne (1921) also noted that the hard parts of the prey are discarded. Moore (1906) noted that *C. purpurea* may return to its adult burrow to eat its prey, that it could seen ants 10 to 13 cm away, and that it rushed up to an ant, bit it once, and gave it a toss, repeating this behavior until the ant showed no signs of life. He also noted that the vision of *C.*

Table 6. Food of *Cicindela* eaten in nature that has been reported in the literature.

- Crustacea—fiddler crabs (young) and marine "fleas" *(C. ocellata)*
- Arachnida—unidentified species of spiders *(C. repanda, C. sexguttata)*
- Insecta
  - Orthoptera
    - Acrididae—*Melanoplus spretus (C. circumpicta, C. formosa, C. fulgida, C. purchra, C. punctulata, C. scutellaris, C. sexguttata, C. tranquebarica); Stenobothrus* sp. (nymph) *(C. silvicola)*
  - Dermaptera—*(C. campestris)*
  - Hemiptera
    - Lygaeidae—*Blissus leucopterus (C. punctulata)*
    - Coreidae—*Leptocoris trivittatus (C. splendida)*
  - Homoptera
    - Aphididae—*(C. tranquebarica)*
  - Coleoptera
    - Carabidae—*Harpalus pennsylvanicus* (*C. sexguttata,* was larger than cicindelid and escaped); *Bembidion* sp. *(C. cuprascens, C. hirticollis)*
    - Heteroceridae—*(C. cuprascens, C. hirticollis)*
    - Elateridae—*Horistonotus uhleri (C. rufiventris)*
    - Coccinellidae—*(C. hybrida)*
    - Tenebrionidae—*Tenebrio molitor (C. hybrida)*
    - Chrysomelidae—*Disonycha quinquevittata (C. formosa)*
      Leptinotarsa decimlineata (small larvae) *(C. punctulata)*
    - Curculionidae—*Phytonomus punctatus ? (C. repanda ?)*
    - Small, unidentified adults—*(C. tranquebarica)*
  - Lepidoptera
    - Phalaenidae—*Pseudaletia unipuncta ? (C. sexguttata)*; unidentified larvae ("cutworms") *(C. scutellaris, C. tranquebarica)*
    - Notodontidae—"puss moth" *(C. campestris)*
    - Galleriidae—*Galleria melonella* (larva) *(C. hybrida)*
    - Pieridae—"white butterfly" *(C. campestris)*
    - Unidentified larvae *(C. campestris)*
  - Diptera
    - Calliphoridae—*Lucilia caesar (C. hybrida); Calliphora volitoria (C. hybrida)*
    - Sarcophagidae—*Sarcophaga camaea (C. hybrida)*
    - Unidentified muscoid larvae and adults *(C. repanda)*
    - "Gnats" *(C. sexguttata)*
    - Unidentified larvae *(C. cuprascens, C. hirticollis)*
  - Hymenoptera
    - Formicidae—*Pogonomyrmex occidentalis (C. fulgida); Formica pallidefulva (C. formosa,* was unsuccessful); unidentified adults *(C. ocellata, C. formosa, C. longilabris, C. punctulata, C. purpurea, C. repanda, C. scutellaris, C. sexguttata, C. tranquebarica)*
    - "Bees"—*(C. tranquebarica)*
    - Halictidae—*Lasioglossum zephyrum* (dead adults) *(C. repanda); Nomia melanderi* (dead adults) *(C. haemorrhagica, C. pusilla)*
- Other
  - Freshly dead carcasses (fish, rabbits, etc.) (*C. ocellata*—this is doubtful; perhaps they were eating carcass-feeding insects)

TABLE 7. Arthropods that adults of *Cicindela* have eaten or attacked in the field (F) and in a laboratory terrarium.

- Arachnida
  - Salticidae (F)
  - Lycosidae ?
  - Small, unidentified species
- Insecta
  - Orthoptera
    - Gryllidae—*Oecantha* sp. (nymph)
    - Tettigoniidae—(nymph over 1 cm long)
  - Hemiptera
    - Gelastocoridae—*Gelastocoris* sp. (F) (attacked, but not eaten)
    - Miridae
    - Nabidae—*Nabis ferus*
    - Lygaeidae—*Ischnoderus falicus*; nymph of another species
    - Cydnidae (F)
    - Pentatomidae (nymph)
  - Homoptera
    - Cicadellidae
    - Aphididae (F)
  - Neuroptera
    - Chrysopidae
  - Coleoptera
    - Cicindelidae—*Cicindela togata*
    - Caradibae—*Anisodactylus* sp. (F)
    - Coccinellidae (could not get a grip on it, unsuccessful)
    - Chrysomelidae—*Ceratoma trifurcata* (F—unsuccessful, apparently distasteful); *Diabrotica undecimpunctata*; Halticinae (unident.); *Monoxia puncticollis* (F—unsuccessful, apparently distasteful)
  - Lepidoptera
    - Pyralidae—*Anagasta kuehniella*
    - Geometridae (larvae)
    - Small, unidentified caterpillars
  - Diptera
    - Stratiomyidae
    - Tachinidae
    - Muscidae
  - Hymenoptera
    - Formicidae—*Pogonomyrmex occidentalis* (F—ant heads found with mandibles clamped on cicindelid antennae or palps); *Crematogaster* sp. (dealate queen) (F)

repanda seems to be limited to 8 to 13 cm, that it takes *C. repanda* four or five minutes to eat a housefly, and that this species seems to be afraid of ants. Huie (1915) reported that a *C. campestris* in captivity ate freshly emerged adults of the same species. Goldsmith (1916) observed that *C. sexguttata* would give up an attack if the prey offered any resistance. He also watched a group of 27 *C. repanda* feeding on a colony of "small red ants." Another time he saw two beetles of the same species devour a whole colony of ants by alternating eating each ant that came to the entrance of the hole; when no more ants appeared, one beetle dug half the length of its body into the mound in search of more food. Swiecimski (1957) studied the role of sight and memory in food capture by *C. hybrida* in terraria, using various types of live and dead insect bait. He found that the beetles obtain food by random search (only immobile prey) or deliberate attack caused by perception from a distance (up to 25 cm); they do not react to dead prey moved artificially, or are frightened. In random search, vision does not play an important part, the beetle often trying to eat pebbles or other inanimate objects. Apparently chemoreceptors do not function until the prey is very close. Naturally moving prey evokes attack, which may be divided into several stages: 1) preparatory attitude, consisting of elevating the front of the body and turning toward the prey, 2) actual attack, consisting of a quick, interrupted run toward the prey, 3) capture, 4) eating the prey. In some cases, certain stages are omitted, usually caused by variations in the behavior or nature of the prey. Memory of the shape and location of the prey appears to play a part occasionally, because when prey was taken from the beetles, they searched the area where it was, or if it was moved, they reattacked it.

Friederichs (1931) found that European species *(C. campestris, C. hybrida, C. silvicola, C. silvatica)* have binocular vision for about 90° of their forward field of vision, and that they react only to movement. This is probably why beetles turn toward their prey before attacking it : to locate it more accurately.

Evans (1965) gave a detailed account of how the food is eaten by *C. hybrida*. The prey is seized with the long distal teeth of the mandibles; pieces of the cuticle may be cut away to reach the soft inner parts. The food is then raked back into the preoral cavity by rotary movements of the laciniae and accumulates in the form of a bolus that may be chewed for some time by the proximal molar portions of the mandibles. The maxillae move only slightly and, together with the labial palps, help to hold the bolus in place. When enough food is accumulated, the mandibles begin to move the food in a rotary motion in the preoral chamber from the mandibles upward and backward, across the cibarial opening, and down between the labial palps. The labial palps may then push the food up to the maxillae to be recirculated. Rows of setae on the hypopharynx and epipharynx strain out solid particles and allow only fluid and very small solid particles to enter the cibarium. Evans found some evidence of extraoral digestion, that is, regurgitation of enzymes from the gut. Lengerken (1929) also supposed that this occurs.

Observations that I have made on the feeding behavior of *C. circumpicta*, *C. duodecimguttata*, *C. fulgida*, *C. nevadica*, and *C. togata* in the laboratory confirm many of the above reports. *C. togata* saw the movements of small spiders (about 2 mm long) from a distance of 2 to 8 cm, and *C. fulgida* saw adult mites *(Androlaelaps casalis)* about 1 mm in diameter from 2 to 3 cm away (the mites are scavengers that probably were carried into the laboratory with the soil). The prey, if it is distant, is approached by a series of short runs; the beetle then lunges at it with the mandibles open. If the prey is small or stops moving, the beetle may miss it and lunge repeatedly, often merely biting the soil. The beetle seems to rely almost entirely on sight; if the prey eludes it in the above manner, the beetle searches "blindly" the immediate area and does not recognize immobile prey until its head is almost directly over it. Once the prey is seized with the distal part of the mandibles, the beetle may become quite excited, running about, holding the prey with its mandibles. Its excitement is often transferred to other beetles in the terrarium, which also run about searching for food or fighting with the successful individual for the prey. Usually the prey is first masticated thoroughly with the distal parts of the mandibles and maxillae. These organs move laterally alternately and gradually work the prey back and forth. This operation takes about two minutes for a small catepillar about 5 mm long and probably serves to break up large sclerites of the prey. Then the food is moved farther back into the preoral cavity for mastication and circulation as described by Evans (1965). This process may take five to ten minutes, and is occasionally interrupted by the mouthparts becoming still and the head and prothorax being protruded slightly. This is interpreted as swallowing. During mastication, the mandibles are moved laterally quite regularly and mechanically at a rate of 80 to 140 times per minute. Finally, a small, compact pellet about 1 mm in diameter is ejected and laid on the substrate by the beetle. After a beetle had eaten an *Anagasta kuehniella* caterpillar, the resulting pellet was put into water and teased apart. It contained the caterpillar's mandibles, masticated head capsule (broken into irregular pieces ranging from 0.05 to 0.25 mm in diameter), and the thin skin, relatively intact and including setae and proleg crotchets. A medium sized prey (about 5 to 8 mm long) takes about five to 20 minutes to eat. Once a *C. togata* was observed to lay down part of a hemipteran, chew on the other part, then pick up and eat the first part. As noted in Table 7, cannibalism occasionally occurred. One *C. togata* was found without a head, the elytra of another was found, and a third was seen being eaten by an individual of the same species. Probably only weak or sick individuals are cannibalized. In captivity, adults will eat an insect the size of *Anagasta kuehniella* once every one, two, or three days.

Defecation consists of deposition on the substrate of a drop of opaque, pinkish or brownish fluid, which eventually dries into a spot of the same color.

THE ADULT—*Drinking.* A number of workers have reported tiger beetles drinking in captivity: Moore (1906), Williams and Hungerford (1914), Huie (1915), Lengerken (1929), and Zikan (1929). Apparently only Mitchell (1902) has seen drinking in nature.

I have occasionally seen *C. duodecimguttata*, *C. fulgida* and *C. togata* drink in the laboratory. Moore (1906) reported that although he provided *C. repanda* with a drinking container, the beetles did not use it, drinking instead from moist sand. My beetles drank both from a Stender dish and from moist soil. In drinking, the mouthparts, mandibles agape, or much of the head is thrust into the water or moist soil for one-half to several minutes. Sometimes soil is bitten to bring the moist soil closer to the mouth. Presumably the water is sucked up by the foregut.

Balduf (1935) thought that cicindelids require water as often as food; however, cicindelids have been seen drinking in nature so infrequently that this is questionable. Probably much water is obtained from the food, and many species frequent the moister parts of their habitats, which probably reduces their rate of water loss.

Mitchell (1902) stated that *C. ocellata* eats algae and fine moss near springs, but it is more likely that the beetles were sucking water from these plants.

THE ADULT—*Burrows and digging.* Many species dig burrows as adults for various purposes. Some hibernate as adults, usually in deep burrows (5-122 cm deep in Canada; Criddle, 1907). During the warm part of the year, many species make shallower burrows in which to spend the night (Davis, 1921; Rau, 1938), and hot or dry weather (Wallis, 1961). Reineck (1923) rainy or cloudy weather (Moore, 1906; Wille and Michener, 1962; Blanchard, 1921; Dengerken, 1916, 1929; Moore, 1906; Mitchell, 1902; Blanchard, 1921), stated that *C. silvicola* does not dig adult burrows, hiding in natural crevices in cold or rainy weather. I have noted, as has Graves (1963), that *C. sexguttata* may take shelter under loose bark. Mitchell (1902) reported that only females of *Megacephala carolina* dig burrows to spend the day (this species is nocturnal), while males hide under logs, trash piles, dead leaves, or bunches of grass. Usually, however, both sexes burrow. Good descriptions of the digging process are given by Moore (1906), Criddle (1907), and Lengerken (1929).

I have noted adult burrows in the field for *C. circumpicta*, *C. duodecimguttata*, *C. fulgida*, *C. hirticollis*, *C. nevadica*, *C. repanda*, and *C. willistoni*, and have made more detailed observations of digging by *C. fulgida* in the laboratory.

In digging, the beetle loosens bits of soil with its mandibles; the soil is then kicked backward under the body by the first, middle, and hind pairs of legs in succession. Soon a pile of loose soil accumulates at the entrance of the burrow, often plugging it. As the beetle goes deeper, it accumulates a small pile of soil directly behind it, then backs up the burrow to push it out the entrance. The beetle may stop occasionally to rest. Most of the burrow is slightly larger than the body width, but the end is larger, to allow the beetle to turn around (it rests facing outward). The entrance is oval and rather ragged in contrast to the round, smooth holes of most larvae. For short stays, the burrow is usually plugged loosely or with a thin plug; hibernation burrows are entirely plugged except for the bottom 10 to 25 cm (Criddle, 1907). The speed of digging depends on the type of soil. In sand, a beetle can dig its body length in a minute (Lengerken, 1929). A *C. fulgida* dug 3 cm in moderately compact clay in one hour. Usually non-hibernation burrows slant gently downward, are more or less straight, and range from 2 to 10 cm deep. Hibernation burrows are more nearly vertical and often crooked, and when in hard soil are shallower than those of the same species in soft soil (Criddle, 1907). In warmer areas, hibernation burrows are not as deep as reported by Criddle; Blaisdell (1912) found 64 *C. senilis* hibernating under three rocks in relatively short, often interconnected burrows. From one to five individuals were in each chamber. More than one individual in the same burrow is uncommon. Criddle (1907) found both *C. duodecimguttata* and *C. tranquebarica* occasionally in the same burrow as *C. repanda*. Moore (1906) sometimes found two or more *C. repanda* in the same burrow. In digging 67 *C. willistoni* from temporary burrows about 3-5 cm long, I found two beetles in the same burrow in only three cases. The burrows were usually plugged except for the bottom 2 cm and had a mound of loose soil over the hole.

C. togata was never seen to burrow in captivity or in the field, although one once spent the night in a *C. fulgida* burrow. They readily take shelter under available objects. Their long legs do not seem to be well adapted for digging.

The Adult—*Cleaning*. Adults frequently clean themselves, as after digging, eating, or drinking. Lengerken (1929) stated that beetles often stop in the midst of digging to clean themselves of sand, and then continue. The front tarsi are rubbed over the front and upper surfaces of the head (simultaneously or one at a time), and the antennae are pulled between the apical tibial spurs and the tarsi of the front legs. The front legs are used to clean the mouthparts and the mouthparts to clean the front legs. Primarily the middle tibiae are used to clean the elytra, although the hind tibiae sometimes assist, by being rubbed quickly over the dorsum. In addition, the distal parts of the legs are cleaned by being rubbed together, two at a time, the first with the middle or the hind with the middle. The front and particularly the middle tibiae bear on their inner apical portions, areas of short, closely set setae that seem to serve for cleaning. When an apparently distasteful insect is seized, a beetle will often dig its mandibles into the soil repeatedly, probably in an attempt to clean them of the offensive substance.

The Adult—*Sleep*. Behavior resembling sleep is known in many insects. No specific mention of sleep in cicindelids is known, although some authors implied that sleep occurs in the burrow or other retreat (Rau, 1938; Davis, 1921; Moore, 1906). In the laboratory, I have on several occasions found adults apparently asleep *(C. fulgida, C. nevadica,* and *C. togata)*. The beetles were motionless in a normal standing position or with the venter resting on the substrate and acted half dead when touched. After several seconds of being prodded, they seemed to "wake up" and became active.

The Adult—*Activity*. Many workers have noted that *Cicindela* tends to be most active on hot, sunny days. Lengerken (1916, 1929) and Shelford (1908) noted that mating occurs only in such conditions (see above section on mating). Reineck (1923), Moore (1906), Huie (1915), and others have noted that beetles remain hidden or in burrows on cool and cloudy or rainy days. Lengerken (1916) reported that even a cloud passing before the sun curtailed the activity of *C. maritima* and *C. hybrida*. Davis (1921) watched a *C. tranquebarica* dig at about 4:45 PM a burrow in which to spend the night. Moore (1906) said that *C. repanda* retires at about 5 PM on ordinary days and about 7 PM if the weather is very warm, and that *C. purpurea* remained active until late in the evening if the day was hot. He also said that *C. repanda* becomes active at about 8 or 9 AM or earlier on very warm days. Remmert (1960) found that *C. campestris* alternates variable periods of rest and activity during the day; hungry individuals have longer periods of activity and shorter periods of rest (and vice versa for full individuals); at higher temperatures or in stronger light, the periods of rest are shorter.

I have noted that on hot days, *Cicindela* is active in spite of clouds; in fact, if the habitat is very hot, activity decreases, the bettles remaining in the shade of vegetation or other objects, or in cracks until clouds come and lower the temperature. More will be said about the effects of physical conditions on activity in a later section.

The Adult—*Fighting*. Huie (1915) noticed that female *C. campestris* in captivity were frequently disturbed by other beetles running into them, pulling their legs, or seizing them by the body (probably mating attempts). Lengerken (1916, 1929) often noted fighting among captive beetles. Sometimes when two individuals met they would stop and elevate the front of their bodies, mandibles open wide; often this apparent threatening behavior averted actual combat. If two individuals ran into one another from opposite directions, they tumbled around together briefly before continuing on their way. Moore (1906) observed fighting in captive and free *C. repanda*. One beetle rushed at another, snapping at it with its mandibles or merely bumping into it and then running away. The other beetle then chased the first for a while. Legs and antennae were sometimes lost as a result of these encounters in captive individuals.

I frequently observed fighting in captive *C. togata* and *C. fulgida*, often for food. Once two *C. fulgida* were seen fighting for a small lycosid spider, one riding on the others back, both chewing on the spider. Another time a female *C. togata* rushed up to a male that had just caught a small spider; they faced one another and fought with their mandibles for about ten seconds; then the female rushed at the male twice before giving up. In the spring when mating occurs, *C. fulgida* are quite aggressive; one often seized another's leg, and they tumbled around for a few seconds. Once a *C. togata* that was in a *C. fulgida* burrow was quickly approached by a *C. fulgida*; they fought briefly with their mandibles, and the *C. togata* remained in the burrow. A *C. nevadica* was found with a broken left hind tibia that it apparently received in a fight, and specimens with tarsi or antennae missing have been seen. In the field, I once saw a number of *C. circumpicta* rushing at one another in the manner described by Moore (1906).

The Adult—*Flying and escape.* Davis (1921) watched a *C. tranquebarica* for an hour and saw it fly only once; and Moore (1906) watched a *C. purpurea* traverse about 40 meters of a road in an hour without flying. These notes confirm the impression that I have received from casual observations that although most species of *Cicindela* have the power of flight, they rarely fly. When going about their usualy activity of preying, *Cicindela* typically runs in short bursts, often in a zig zag course. Usually only when disturbed by a larger animal do they fly, and even then some species (or under certain conditions) fly only as a last resort.

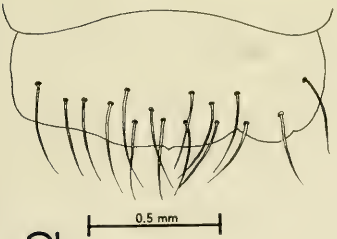
As Moore (1906) noted, before flying, a beetle squats close to the ground. If further frightened, the beetle jumps into the air and takes wing (Moore remarked that deformed beetles unable to fly could jump about 3 cm high). Several authors have noticed differences in the flying abilities and habits of different species. Most species of *Cicindela* fly in a low (1 to 2 m), level path and land 5 to 15 meters from the source of disturbance. Some early authors thought that beetles always landed facing the source of danger, but later observations showed that they land facing the wind (Moore, 1906). Often a beetle will circle and land behind the disturbance, particularly if flushed repeatedly. More intricate midflight maneuvers may be made, if the beetle "sees" it is about to land in unsuitable territory, to bring it to a "desired" landing place.

As implied above, escape behavior varies with the species, the external conditions, and the degree of danger. Moore (1906) noted that *C. purpurea* usually flew only a short distance down a road unless persistently pursued; then they flew into the nearby grass, ran to a clear space, and either flew again or squatted ready to fly. *C. togata*, a species with long legs, often tries to outrun the danger. If hard pressed, it usually runs in a zig zag course and may run into short, sparse *Distichlis* grass rather than fly. When it does fly, it frequently flies into dense grass. The same zig zag running behavior has also been noticed in *C. circumpicta*, and this species was also seen to fly or run into vegetation to escape. *C. fulgida*, which is normally found among sparse vegetation, usually flies at the slightest danger, often into dense vegetation, but sometimes out onto a bare salt flat. Sometimes species that are surprised in short vegetation have difficulty flying because of bumping into the plants. *C. hirticollis* is another very wary species that is difficult to capture. String wind and low temperature generally deter or inhibit flying.

THE ADULT—*Injuries and deformities.* As mentioned above, injuries are sometimes inflicted by other cicindelids. Townsend (1884) mentioned finding *C. tranquebarica* with antennae, legs, or elytra injured or missing. I have collected specimens with injuries that probably were not caused by fighting. A *C. fulgida* was collected with both hind tibiae and tarsi missing, a *C. togata* was found with the tip of one elytron missing, and a *C. circumpicta* was found on its back, legs kicking, with its entire abdomen missing. Probably predators inflicted these injuries.

Several authors have reported deformities in cicindelids. Moore (1906) noted that some *C. purpurea* have fused elytra and cannot fly. Townsend (1884) found a *C. tranquebarica* with a wrinkle across one elytron and noted (as I have) that some individuals of this species cannot fly. Horn (1927) reported atypical elytral markings, short elytra, deformed leg segments, and a deformed head and prothorax in *Cicindela* and several other genera. Shelford (1913c) showed atypical patterns of elytral tracheation in *Cicindela.* Shelford (1915) noted that leg and antennal abnormalities are rare, while elytral and labral abnormalities are more common in nature. He also experimentally produced deformities by injuring larvae and pupae of *C. punctulata*; injuring the pupal labrum produced adult deformities, but injuries to the pupal legs or larval labrum had little or no effect on the adult. He thought that elytral deformities such as an abnormally short elytron (often accompanied by reduced markings) or holes in the elytron were caused by injuries to the pupal elytra. I have occasionally found labral and elytral deformities in *Cicindela*; some of these are shown in Figures 81-84.

Wood (1965) found a *C. scutellaris* with a trifurcate ninth antennal segment (each fork having two additional segments), and noted that similar abnormalities have been reported in a cerambycid. Park (1931) and Lavigne (1965) found them in a tenebrionid and cerambycids. I collected a *C. nevadica* with a similar deformity, Figures 85 and 86. The third segment of the left antenna is bifurcate at the apex, and segments four to eleven are duplicated.



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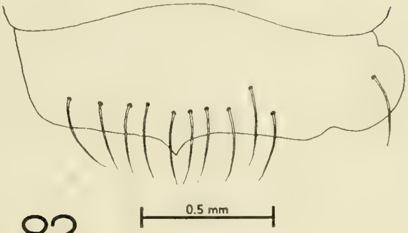

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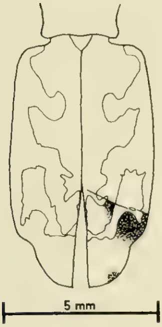

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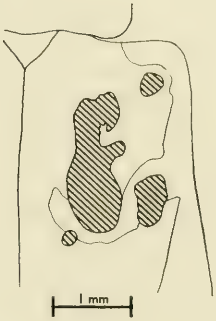

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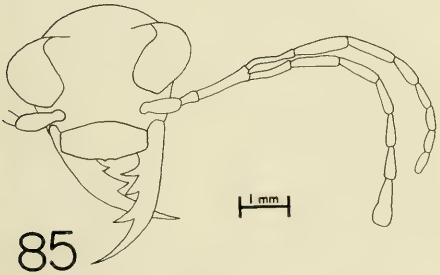

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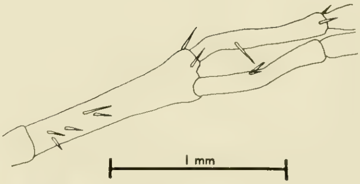

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Fig. 81. Deformed labrum of male *C. nevadica nevadica*, from Saltdale, Kern Co., California, frontal aspect. Fig. 82. Deformed labrum of male *C. nevadica knausi*, from 2.5 mi. southwest of Plainview, Woods Co., Oklahoma, frontal aspect. Fig. 83. Normal (left) and deformed (right) elytra of female *C. nevadica olmosa* (paratype), from 25 mi. west of Tularosa, Sierra Co., New Mexico, dorsal aspect; a crease runs transversely across the right elytron, interrupted by a small hole near the margin; stippled areas are discolored (light brown), normally white maculation. Fig. 84. Anterior half of right elytron of female *C. nevadica knausi*, from 1 mi. northeast of Tucumcari, Quay Co., New Mexico, dorsal aspect; shaded areas represent holes; the posterior portion of the humeral lunule (caudad from largest hole) is atypical (see Fig. 83 for typical humeral lunule). Fig. 85. Head and deformed left antenna of male *C. nevadica knausi*, from 3 mi. east of Cherokee, Alfalfa Co., Oklahoma, cephalic aspect. Fig. 86. Enlargement of third and duplicated fourth segments of same.

The Adult—*Odor*. It has often been mentioned in the literature (e.g., Leng, 1902; Eckhoff, 1939; Graves, 1963) that *C. punctulata* emits a fruity or applelike odor when handled. Leng (1902) also reported that *C. sexguttata* emits a fragrant odor and *C. longilabris* a musky odor when captured. Lengerken (1929) noted a pleasant odor produced by *C. maritima* in hot weather and when the beetles were alarmed, as when captured. I have noticed that *C. ocellata* and *C. tranquebarica*, when handled, emit an odor similar to that of *C. punctulata*, but weaker, and that *C. duodecimguttata* produces a musky odor.

These odors are produced by the anal, or pygidial glands. Dierckx (1899, 1901) discussed the anatomy of these glands in *C. hybrida* and *C. campestris*, noting that they are similar to those of carabids, with an oval, cuticular, sparsely muscled reservoir; a collecting canal; and a long, cylindrical gland proper. Brandt (1888) remarked that the anal glands of cicindelids (no species given) are more poorly developed than in carabids because the cicindelids have other well developed means of escape (running, flying) and defense (mandibles). Although the subject has not been studied further, Brandt's explanation is probably correct.

THE ADULT—*Sound production.* Certain cicindelid genera, *Mantica*, *Mantichora*, *Oxychila*, and *Chiloxia*, possess stridulatory organs, ridges on the margins of the elytra and hind tibiae (Horn, 1908-15). I have noticed that captive *Cicindela (C. fulgida, C. nevadica)* sometimes raise their elytra synchronously very slightly once or several times. Sometimes when this is done, faint but clearly audible sounds are produced, best described as short buzzes. Captive *C. repanda* have been heard making a continuous buzz lasting about one second while the elytra were raised slightly. Apparently the sound is produced by slight irregularities on the elytra where they join, although none are readily visible under magnifications of about 80X. The sound is probably purely accidental.

Sound is also produced in flying species when the wings beat. It is usually not audible to humans except in the larger species, in which a low buzz can be heard as the beetle takes off.

THE ADULT—*Predators and parasites.* Relatively few records of enemies of adult cicindelids have appeared in the literature. Ingram (1934) found a mite (unidentified) parasitic on the thorax and legs of *C. haemorrhagica*. Graves (1962) watched a dragonfly, *Aeshna interrupta*, catch a *C. repanda* in flight and carry it away. Asilid flies seem to be the most common predator: Fox (1910) reported them catching and eating *C. dorsalis*; Fackler (1918) saw a *Proctacanthus* (near *rufus*) catch a *C. repanda*, inserting the proboscis between the elytra to feed; Bromley (1914) saw *Proctacanthus philadelphicus* eat *C. punctulata*, on three different occasions, and once saw *Promachus fitchi* catch the same species; Davis (1910) saw a *C. sexguttata* caught and eaten by a *Laphria* sp., about as large as the beetle; Wallis (1913, 1961) reported *Proctacanthus milberti* catching a *C. purpurea* and inserting the proboscis between the elytra to feed, as well as asilids twice catching beetles in flight; Stevenin (1948) saw an asilid repeatedly attack a *C. apiata* in Uruguay.

Blaisdell (1912) found evidence that lizards eat *C. senilis*. Zikan (1929) said that chickens and a "wren" may eat adults. Fackler (1918) reported that the remains of *Amblychila* had been found in a hawk's stomach; Fitch (1963) found remains of *Cicindela* in pellets of the Mississippi kite. Criddle (1907) said that badgers sometimes destroy large numbers of adults; Snow (1877) found a freshly eaten *Amblychila* in the stomach of a skunk; Stains (1956) reported fragments of *Cicindela* in scats of the raccoon.

Many of the *C. circumpicta* I collected on 28 August 1963 from near Drummond, Garfield County, Oklahoma, were heavily infested with larval mites of an undescribed species of *Eutrombidium* (Trombidiidae). Most of the mites were under the elytra, on top of the abdomen, and on the hind wings; a few were on the venter of the abdomen. The infestation was apparently only "accidental" because these mites have not been found on the same species from that locality in later years, nor from beetles from other localities. This genus of mites lives in the soil as nymphs and adults, eating orthopteran eggs; larvae have been found parasitizing several genera of orthopterans (Evans et al., 1961). I have also found a number of mites (Uropodidae) attached to the thorax and legs of two museum specimens of *C. sexguttata*. This family of mites is not actually parasitic, but phoretic, attaching to insects in the deutonymph stage for transportation (Evans et al., 1961).

I have twice caught asilids eating *Cicindela*: *Diogmites symmachus* with a *C. togata*, and *Proctacanthus milberti* with a *C. formosa*. Asilids are often common in and near saline habitats.

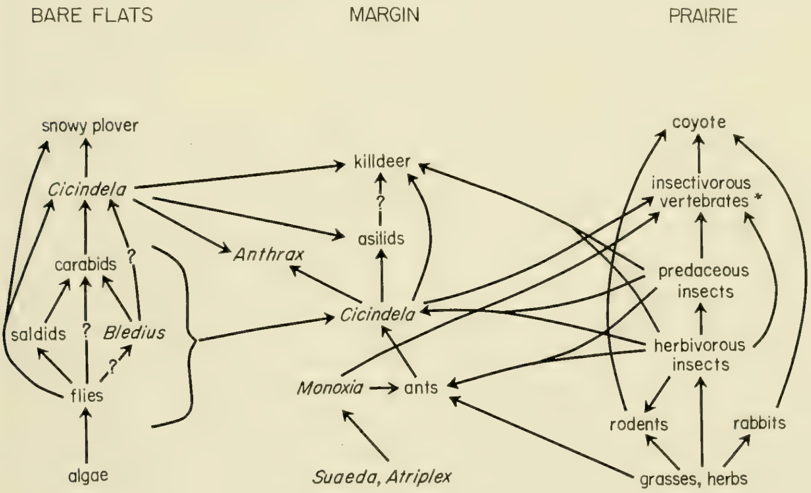
On a small salt flat in north central Kansas, I found two regurgitated pellets about 1 cm in diameter, which an ornithologist, Dr. Richard J. Johnston, thought were produced by a sparrow hawk. They contained remains of insects: a bee, a carabid, several chrysomelids, and three species of cicindelids, *C. circumpicta*, *C. togata*, and *C. punctulata*. Other birds which eat insects, such as killdeers and snowy plovers, are often common in saline habitats and likely eat some *Cicindela*.

THE ADULT—*Ecological relationships.* Certain of the relationships of cicindelids with other animals have been discussed in the sections on food and predators and parasites. Other arthropods, besides *Cicindela*, that I have seen or collected in saline habitats are listed in Table 8. These relationships can be summarized in a diagram (Fig. 87), showing the interactions of the major organisms in a saline habitat. Saline habitats and their assemblage of organisms could be considered ecological communities, since their organisms show a certain amount of interdependence and function somewhat as a unit. However, as can be seen from Figure 87, there is also an intimate connection between the saline habitat and the surrounding prairie. Because of this, the saline habitat should more properly be called a minor community.

TABLE 8. Arthropods, other than *Cicindela*, seen and collected in saline habitats in the central United States.

- Crustacea
  - Isopoda
- Diplopoda
- Arachnida
  - Acarina (infesting *Cicindela*)
  - Araneida
- Insecta
  - Odonata
    - Libellulidae, Gomphidae, Aeshnidae, Coenagionidae
  - Orthoptera
    - Acrididae, *Trimerotropis* sp.
    - Tetrigidae, *Paratettix* sp.
    - Tridactylidae, *Tridactylus minutus*
  - Hemiptera
    - Gelastocoridae, *Gelastocoris oculatus*
    - Saldidae, *Pentacora signoreti*
    - Cydnidae, *Schirus cinctus*
    - Pentatomidae, *Rhytidolomia* sp.
  - Homoptera
    - Fulgoridae, *Scolops* sp.
  - Coleoptera
    - Cicindelidae, *Megacephala virginica*
    - Carabidae, *Agonoderus lineola, A. obliqulus, Anisodactylus* sp., *Aspidoglossa subangulata, Bembidion coxendix, Calosoma* sp., *Clivina dentipes, Cratacanthus dubius, Diplocheila assimilis, Dyschirius criddlei, Elaphrus ruscarius, Geopinus incrassatus, Harpalus amputatus, H. pennsylvanicus, Pogonistes planatus, Pterostichus sayi, Scarites substriatus, Selenophorus* sp., *Tachys* sp.
    - Omophronidae, *Omophron nitidus*
    - Staphylinidae, *Bledius* sp.
    - Histeridae, *Hister biplagiatus*
    - Meloidae, *Epicauta conferta, E. segmentata*
    - Tenebrionidae, *Eleodes hispilabris, E. opaca, Lobometapon* sp.
    - Scarabaeidae, *Cotalpa subcribrata*
    - Chrysomelidae, *Calligrapha sp., Leptinotarsa decimlineata, Monoxia puncticollis*
    - Curculionidae, *Cleonis angularis, Hypera punctata, Lixus* sp., *Ophryastes vittatus, Pantomorus pallidus, Phytonomus nigrirostris, Sphenophorus aequalis, S. australis, S. callosus, S. destructor, S. germari, S. parvulus, S. scoparius, S. venatus*
  - Diptera
    - Chironomidae
    - Ceratopogonidae
    - Culicidae
    - Tabanidae, *Chrysops vittatus*
    - Stratiomyidae, *Eulalia communis*
    - Bombyliidae, *Anthrax analis, Exoprosopa dodrans, E. sordida*
    - Asilidae, *Diogmites symmachus, Laphystia* sp., *Nerax* sp., *Proctacanthus milberti*
    - Dolichopodidae
    - Syrphidae, *Eristalis aeneus, Eupeodes* sp.

Otitidae, *Cheroxys latiuscula*
Ephydridae, *Ephydra* sp.
Sarcophagidae
Muscidae
Anthomyiidae
Hymenoptera
  Tiphiidae, *Pterombrus rufiventris, Myzinum quinquecinctum*
  Mutillidae, *Dasymutilla leda, D. occidentalis, D. quadriguttata, D. vesta, D. waco*
  Formicidae, *Crematogaster* sp., *Pogonomyrmex occidentalis, Prenolepis imparis*
  Sphecidae, *Ammophila varipes, Cerceris* sp., *Prionyx atratus, Stigoides unicinctus*
  Pompilidae, *Anoplius* sp., *Poecilopompilus interruptus*
  Andrenidae, *Calliopsis* sp.
  Anthophoridae, Eucerinae


BARE FLATS
MARGIN
PRAIRIE
snowy plover
Cicindela
carabids
?
saldids
?
Bledius
?
flies
algae
killdeer
?
asilids
Anthrax
Cicindela
Monoxia
ants
Suaeda, Atriplex
coyote
insectivorous vertebrates *
predaceous insects
herbivorous insects
rodents
rabbits
grasses, herbs

87

*toads, lizards, sparrow hawk, raccoon, badger

FIG. 87. Interrelations of the major organisms in a salt flat community (subdivided into bare flats and margin) and the surrounding prairie. The organisms that the arrows point to use those at the other ends for food.

Another sort of relationship between cicindelids and other animals is found in the closely related phenomena of mimicry and cryptic coloration, in which a species evolves to look or act like something inedible (or at least not high on the list of "preferred" foods) to a predator species. R. Shelford (1902) and Robinson (1903) discussed some instances of mimicry of tropical Asian cicindelids (*Tricondyla, Collyris, Cicindela*) by locustids, cerambycids, a sciomyzid fly, and wasps. Blickle (1958) reported that a species of tabanid in Florida resembles *C. dorsalis* in color and flight habits.

Townsend (1886) noted that the species that live in wooded areas, such as *C. sexguttata*, are often green and difficult to see, even when sitting on a log; while others that frequent bare soil (*C. macra*, *C. cuprascens*, *C. repanda*, *C. tranquebarica*, and others) are often the same color as their background. He also noted that the white elytral markings, rather than being conspicuous, break up the outline of the insect and make it even harder to see; and that the ventral coloration, not visible from above, is often more brilliant than the dorsum. Wallis (1961) also mentioned matching of the background color, citing the nearly white species, *C. lepida*, which inhabits light sand and whose shadow is often more conspicuous than itself. Fox (1910) noted the close resemblance of some species on the New Jersey coast to their background, but also noted that in two species, individuals sometimes occurred on the "wrong" background. N. L. Rumpp *(in litt.)* said that two subspecies of *C. willistoni (pseudosenilis* and *praedicta)* are not at all well camouflaged, being dark blue-green forms and occurring on white salt pans in the Mojave Desert.

I too have noted that individuals of many species are very difficult to detect against their natural background, particularly when they do not move. Of the approximately 80 species of *Cicindela* in the United States, over 50 have a rather dull (brownish, blackish, dark green) dorsal color, over 20 are dull in some parts of their ranges and bright in others, and only about five are consistently bright (of these, two are green woodland forms). Of about 35 species that I have collected, about 25 are well camouflaged, five are well camouflaged in some parts of their ranges or in certain polymorphic forms, and only a few do not match their background well. It is interesting that in some species which appear dull to the naked eye (e.g., *C. macra*, which appears brownish), the elytral color, when viewed through a microscope, is actually made up of spots of bright blue or green on a red background; if the blue or green spots are large, the beetle appears dark brown, and if they are small, the color is bright reddish brown.

It seems likely that many of the predators of *Cicindela* exert a selection pressure that results in the beetles resembling their background by the killing of ill-matched individuals. Many birds and insects are known to have color vision. Evidence that this occurs is found in the sparrow hawk pellets that I examined (see section on predators and parasites). Remains of *C. circumpicta*, which occurs in reddish, green, and blue color forms in Kansas, were present; all were of green individuals, even though over 60% of the individuals are reddish in that area.

The pattern of geographic variation of color in some species (particularly *C. togata*) has led me to hypothesize that certain species of saline habitats respond to two selection pressures: one, to match the color of the soil in their local area; and two, to match the white of the salt. As noted in the section on saline habitats, in dry weather saline habitats become covered by a crust of crystalline salt; however, in wet weather the salt dissolves and the color of the underlying soil appears. Thus, the *Cicindela* of these habitats live on a substrate that frequently changes color. In many of the species in this study (*C. circumpicta*, *C. cuprascens*, *C. hirticollis*, *C. macra*, *C. nevadica*, *C. togata*, and *C. willistoni*), I have noticed a definite correspondence between the dorsal coloration and the color of the soil in the locality. This is investigated more thoroughly in later sections. In the most nonfluvial species, *C. togata*, there is a decrease in the amount of white on the elytra in the eastern parts of the range, where the climate is more humid; while the southwestern part of the range, where the soil is more often dry, the white of the elytra increases. In one locality in western Texas, where the soil is nearly white, the elytra are almost completely white. This great tendency of some species to match their background can sometimes be used as a clue to past dispersals or ranges of these species.

In most species, the dorsum of the abdomen (as well as the venter of the body) is a bright metallic color, usually green or blue, even if the rest of the dorsum is dull. When the beetles fly, this bright area of the body is suddenly visible as the elytra are raised. It is possible that this acts as a flash or startle coloration to predators.

The species in this study exhibit certain morphological, physiological, and behavioral traits, or adaptations, for living in saline habitats, listed in Table 9. Some species have more or different adaptations than others. Since few

TABLE 9. Important morphological and behavioral traits for living in saline habitats (L=found in larvae also). Not all traits are necessarily found in all species studied.

Those shared with species not found in saline habitats;

1. Inactivity during the least favorable parts of the year (winter, summer); L.
2. Dig burrows to withstand temporary harsh conditions (storms, daily temperature fluctuations).
3. Hide under vegetation, in cracks, etc., to escape heat.
4. Protective coloration (resemble color of substrate, white markings act as disruptive coloration).
5. Cuticle of adult and setae of larvae protect from salt.
6. Reduction of competition (spatial and temporal segregation), L.
7. Able to be active at high temperatures; L.

Those found primarily in species of saline habitats:

8. Long legs:
    a. For rapid running to catch prey and escape enemies.
    b. To elevate body higher above hot substrate.
9. Increased white markings and body setae; L.
10. Tend not to fly because of high winds.

of the adaptations are restricted to species of saline habitats (even increased white on the body is found in some species living on light sand), probably few evolutionary changes were necessary for these species to become adapted to saline habitats. Those modifications that are necessary apparently have developed repeatedly, for many relatively unrelated species or species groups throughout the world are found in saline habitats. The first-listed adaptation, inactivity during the least favorable parts of the year, could be either an advantage or a disadvantage; if a species could become adapted to being active during the hot, dry summer, it could avoid competition from other cicindelids, provided there was sufficient food to make this a "worthwhile" expenditure of energy.

The literature is replete with notes about habitats in which adult cicindelids are found, and no attempt will be made to review them all. Blanchard (1921) found definite habitat preferences for 11 species in Michigan, and Fox (1910) did the same for 11 species in New Jersey. Sherman (1908) noted different species occurring at different elevations in western North Carolina. Vaurie (1950) gave brief habitat notes for 27 species in north central North America. In general, some species are found in quite restricted habitats, while others frequent many types of habitats. Such factors as the type and moisture of the soil, amount of vegetation, disturbance of the habitat, and climate are important in determining whether a species will inhabit an area.

One notable characteristic of many saline habitats in the central United States is that they support numerous species and individuals of *Cicindela*. On one June morning I collected 11 species (some being abundant) within an area of about one acre on a large salt flat in Woods County, Oklahoma. This is one extreme, but many habitats have five or more species. According to the competitive displacement principle (Gause's law), different species having identical ecological niches cannot coexist for long in the same habitat (DeBach, 1966); therefore, one naturally wonders how all these species can exist together, since all are general predators of about the same size, and since food appears to be scarce in saline habitats. By collecting throughout the warm months and noting the distribution of species in a particular saline habitat, I have found that there is a tendency for the species to be separated both spatially and temporally.

Spatial segregation is effected by the preference of various species for different microhabitats. This phenomenon is shown graphically in Figure 88, where species most likely to be active at the same time of year are grouped together. Clearly, some species, (*C. cuprascens*, *C. duodecimguttata*, *C. hirticollis*, *C. macra*, *C. nevadica*, and *C. repanda*) "prefer" moist conditions, one (*C. togata*) is most common on bare salt flats, one (*C. fulgida*) is common in dry, vegetated areas, and others (*C. circumpicta*, *C. punctulata*, and *C. willistoni*) are found in a variety of habitats. Another sort of spatial segregation

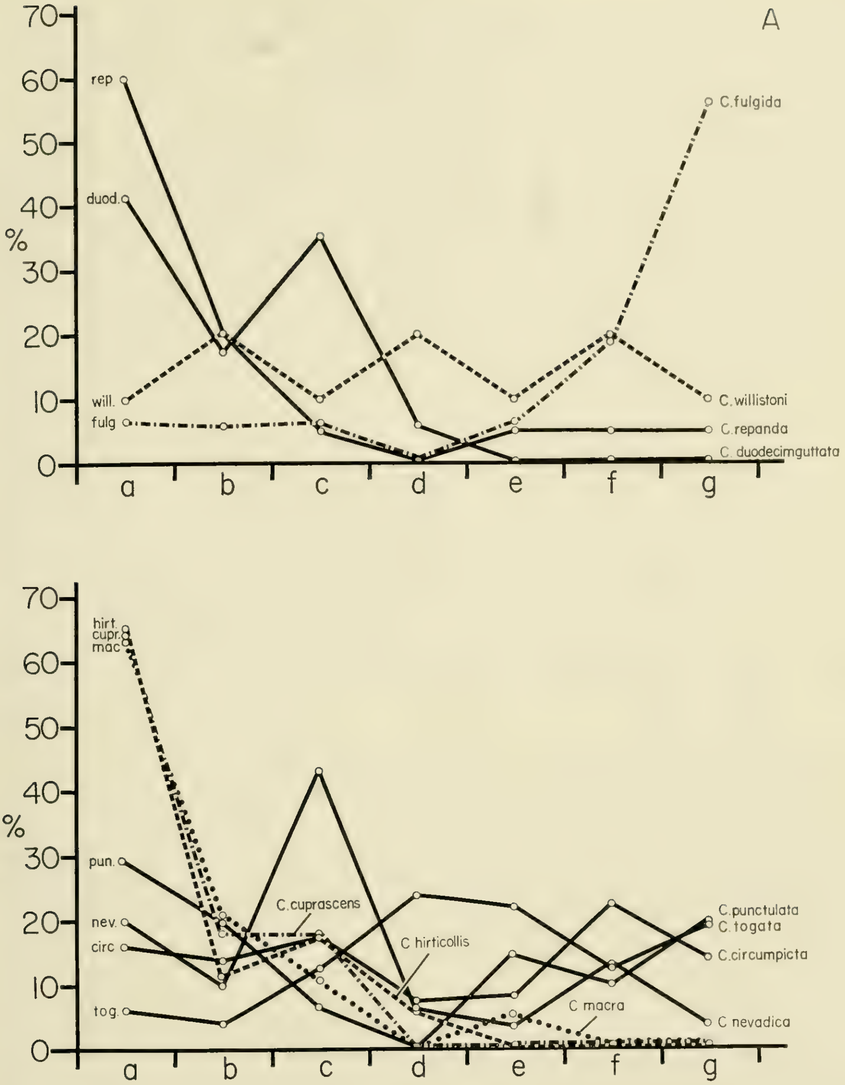


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FIG. 88. Per cent of instances in which the species were noted in various microhabitats, arranged from wet to dry and vegetated; A=spring and fall species; B=summer species; sample sizes range from 10 to 80, most being above 15; microhabitats: a=near water, or sand bar, b=low wet area, or moist ditch, c=near creek, or creek bank, d=moist bare salt flat, e=dry bare salt flat, f=small flats, or near margin, g=near hummocks, or among vegetation.

is found in differential soil preference. One species *(C. duodecimguttata)* is nearly always found on clayey soil, while some *(C. cuprascens, C. hirticollis,* and *C. macra)* occur on sandy soil. The others seem to have no "preference" and are found on both types of soil.

Temporal segregation is shown in Figure 89, where nonfluvial and fluvial species are grouped together. Some species *(C. duodecimguttata, C. fulgida, C. repanda,* and *C. willistoni)* emerge in the spring after hibernating as adults, mate, oviposit, and die out during the summer; in the fall a new brood of adults emerges. In other species *(C. circumpicta, C. cuprascens, C. hirticollis, C. macra, C. nevadica, C. punctulata,* and *C. togata)*, the adults emerge during the summer, often nearly all at once *(C. nevadica)*, and sometimes show a lull during the hottest months and a smaller emergence in the fall *(C. circumpicta)*.

No diurnal temporal segregation was observed. Adults seem to be active throughout the day in fair weather when the air temperature is above 20° C and below 37° C. One would expect to find from a careful study that the spring and fall species are active at lower temperatures than summer species (see below). This could produce some diurnal temporal segregation during parts of the year when these two types of species occur together.

Although the temporal and spatial segregation are only partial, the combination of the two provides nearly complete separation of some species and

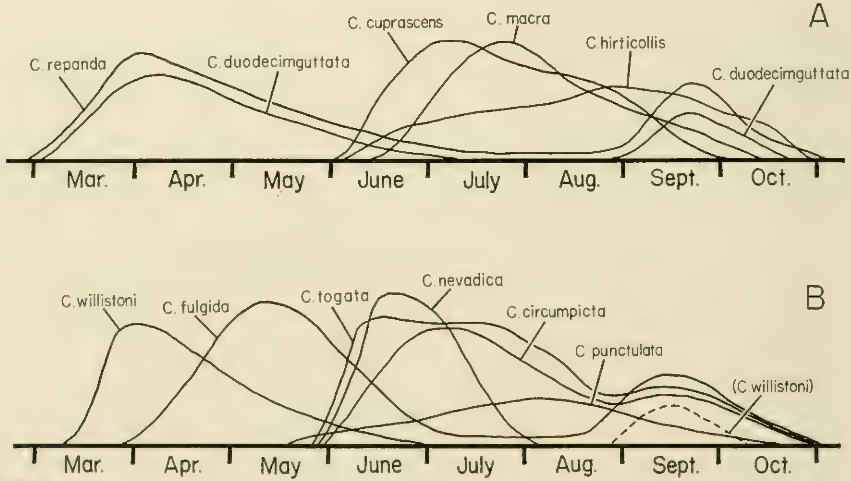

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FIG. 89. Relative abundance of the species throughout the year, generalized from data from localities in southern Kansas and northern Oklahoma; A=fluvial species, B=nonfluvial species; the exact positions of the peaks and ends of the curves, and their heights vary from year to year and at different localities and latitudes; *C. willistoni* has not been collected in the fall, but should be active.

partial separation of others, thus considerably reducing the possibility of competition. No organized data were collected on the subject, but casual observations indicated that food is the most important resource of the environment that is in short supply. Small arthropods suitable for food are usually very uncommon in saline habitats, and only very rarely was an adult or larva seen eating. Since the larva is the primary feeding stage and lives much longer than the adult, no doubt competition for food is even more severe among larvae than adults; furthermore, adults often occur in the same microhabitats as larvae and thus compete with them. Perhaps the long life of larvae and their habitat of lying in wait for prey at night are evolutionary "efforts" to reduce larval-adult competition. Insufficient data are available for the larvae, but it appears that those of most species are active at the same times of year as the adults; however, in species whose adults emerge only in the summer, the larvae are active in the spring as well. Many larvae of *C. togata* are active throughout the hottest part of the summer, when the larvae of most species are inactive (i.e., have their burrows plugged).

Another resource that could be in short supply for species frequenting marginal microhabitats is space, initially for oviposition sites, but ultimately space for larval burrows. Many times I have seen favorable larval sites literally riddled with larval burrows.

If competition among species of *Cicindela* is important, one would expect to find fewer species in habitats with fewer or less abundant resources. In Table 10, the number and abundance of species in 14 saline habitats with varying types and abundance of microhabitats are compared. Those habitats with many microhabitats, abundant water, and a large area have more species which are more abundant than the more impoverished habitats. There are other possible reasons why certain of the habitats in Table 10 have fewer species than others: some are fluvial habitats and would have few if any nonfluvial species; and some of the habitats are outside the ranges of some species. However, it is likely that the "preference" of different species for different microhabitats and the differing ranges of species evolved at least partly because of competition.

Some of the effects on *Cicindela* of physicochemical factors of the environment have been alluded to above. The primary factors that govern the activity of adults seem to be temperature, humidity (actually evaporation), probably light, and wind. Shelford (1913b) found that *C. scutellaris* reacted negatively to dry air and positively to moister air, and that beetles moved against a stream of warm air (in the laboratory). Chapman et al. (1926), in a study of sand dune insects in Minnesota, found that *C. formosa* and *C. lepida* become active at 15-20° C, and that *C. lepida* dies at 45-50° C and *C. formosa* at 50-55° C. They emphasized temperature and noted that the "successful" sand dune insects are able either to endure great extremes or

TABLE 10. Presence and abundance of various microhabitats at 14 saline habitats in southern Kansas and northern Oklahoma (O=absent, pluses indicate relative abundance), and number of species of *Cicindela* and their relative abundance at these habitats (N=total number of species).

Localities (nearest town)	Microhabitats				Number of species				
	Permanent water	Large, open flats	Dry margin or small flats	Short vegetation	Abundant	Common	Uncommon	Rare	N
Plainview, Okla.	+ + + + +	+ + + + +	+ + + +	+ + + +	3	1	1	4	11
Hudson, Kans.	+ + + +	+ + + + +	+ + + +	+ + + + +	4	1		2	9
Cherokee, Okla.	+ + + +	+ + + + +	+ + + +	+ + +	4	1	1	2	8
Hazelton, Kans.	+	+ +	+ +	+ +		2	3	1	6
Geuda Spgs., Kans.	+ + +	O	+	+			3	4	7
Drummond, Okla.	+	O	+	+		3		2	5
Belvidere, Kans.	+	O	+	+		2	2	2	6
Mayfield, Okla.	+ + +	O	+	+		2	1	3	6
Okeene, Okla.	+ + +	O	+	+			4	3	7
Guthrie, Okla.	+ + +	O	O	+	2	1		1	4
Orienta, Okla.	+ + +	O	O	O			2	1	3
Galva, Kans.	+	+	+	O		1		3	4
El Dorado, Kans.	+	+	+	O		2	1	1	4
Greenwich, Kans.	O	+	+	O			1	1	2

avoid them by being active at other times. Rensch (1957) found similar ranges of activity for *C. hybrida* in Europe (25-45° C), *C. bicolor* in India (25-43° C), and *C. nilotica* in Egypt (27-37.5° C). He noted a few individuals of the latter species active on moist sand at 46° C, but never any on dry sand at 43-46.5° C. Remmert (1960) studied daily changes of light and temperature preference in *C. campestris* in the laboratory, finding that during the day the preferred temperature is 34.6° C, while at night it is 26.0° C; however, the temperature preference depends on the physiological state of the beetle: hungry and thirsty individuals have a lower preference than fed ones. His experiments indicated that the beetles are more positively phototactic during the day, but he did not keep temperature and humidity constant, and the results are not conclusive. Payne (1964) studied temperature preferences (humidity not controlled) of *C. repanda* and *C. rufiventris* in the laboratory. *C. repanda*, a spring and fall species, preferred 25-32° C, and *C. rufiventris*, a summer species, preferred 25-38° C.

I have made a few incidental measurements of temperatures at which *Cicindela* become active or cease activity in the field: *C. repanda* was seen "sunning" but not running about when the air temperature was 15° C; *C. duodecimguttata* became active at about 25° C; *C. willistoni* became active at about 18-19° C; *C. circumpicta* was active at about 21° C, and became inactive (in shade of vegetation) at about 36° C; *C. togata* was sluggish and unable to fly at 22° C; *C. punctulata*, *C. circumpicta*, *C. togata*, and *C. repanda* were found near water, in grass, in burrows, or in cracks in the soil at about 38-39° C. As mentioned above, I found *C. circumpicta* mating at night, probably because the habitat was too hot during the day; thus temperature seems to be more important than light in influencing activity. Adults of some species (*C. circumpicta*, *C. cuprascens*, *C. macra*, *C. nevadica*, *C. punctulata*, *C. schauppi* and *C. togata* in this study) also are attracted to artificial lights, making this a profitable means of collecting.

Another effect of temperature (as well as humidity) on adults of certain species was investigated by Shelford (1917). He found that the color and elytral pattern of the adult are affected by the temperature and humidity at which the prepupal and pupal stages develop. Individuals reared at high temperatures had more reduced markings (cover a smaller portion of the elytra) than those reared at low temperatures. Similarly, colors were brighter in dry conditions and darker in moist conditions. He noted that in some species, forms with bright colors and reduced markings occur in hot, dry areas, while forms with bright colors and expanded markings occur in areas of hot, moist climate. However, he noted the importance of microhabitat conditions, which still have not been studied or mapped well.

As mentioned above, strong wind reduces the tendency of some species to fly; when they do, they are often carried to unsuitable habitats. The other effects of wind have not been studied, but no doubt one is increase in rate of water loss, probably causing many species to seek protected microhabitats.

Cicindelids do not seem to be adversely affected by the high concentration of salts in saline habitats. Adults, as well as larvae, of at least some species are found in all parts of saline habitats that are not well vegetated or flooded. Apparently the thick exoskeleton of adults and the long spines and setae of larvae and pupae serve as a mechanical protection from salts.

THE ADULT—*Dispersal.* Besides being the reproductive stage, adult *Cicindela* are the dispersal stage of the species. The fluvial species, none of which is restricted to saline habitats, almost certainly disperse along streams. However, nonfluvial saline habitats are today separated by many miles of land that is unsuitable for species of saline habitats. Yet these species are found at most of them, including man-made ones near oil wells that could not have been in existence for more than 80 or 90 years. How has this dispersal taken place? Although most species of *Cicindela* are agile fliers, they rarely fly in nature unless disturbed by an animal larger than themselves. I have noted that in strong wind, when the beetles do fly, they sometimes lose control and go sailing out of sight over the prairie. Quite probably, strong winds are a factor in dispersal. Storms may or may not be important; adults usually take cover and become inactive in bad weather, although Woodruff and Graves (1963) thought hurricanes might have been responsible for the introduction of a Cuban species into Florida. Between the major saline habitats are scattered many small salty patches, not ideal habitats for large populations of *Cicindela*, but able to support small numbers. Such areas no doubt form "stepping stones" for dispersal between major saline habitats. For example, I have found small populations of *C. circumpicta*, *C. fulgida*, *C. nevadica*, and *C. togata* in small salty spots in pastures and fields. Another factor in some cases is that some nonfluvial saline habitats are interconnected by streams. Species that "prefer" salt flats have occasionally been found on sand bars of streams and evidently disperse along them.

After some beetles have dispersed to a saline habitat, what are the factors that determine whether they can survive there, and if so, how numerous can they become? One of the most important factors is that the soil be of the proper type and moisture content for larval development. Many small salty patches in pastures and roadside ditches become too dry in the summer for the larvae of most species. In some parts of the country (the desert Southwest), extremes in temperature might be a limiting factor, but in the central United States, most species escape unfavorable temperatures by becoming inactive or seeking a microhabitat that is more equable. However, there are some species in the northern United States and western mountains (e.g., *C. pusilla*) which probably do not occur as far south or east as Kansas at least partly because of high temperatures. The availability and abundance of food are obvious and important limiting factors, as is the amount of vegetation. Competition, discussed above, is another. No doubt a combination of these factors is responsible for the decrease in abundance and number of species on impoverished habitats noted above (Table 9). Salinity seems not to affect the beetles at all adversely, since they are found (larvae and adults) in all bare parts of saline habitats.

Man has no doubt had a great effect on the distribution and abundance of cicindelids. By altering or destroying habitats, such as cutting forests or plowing prairies, he has restricted the distribution of some species and made it possible for others to expand. Dirt roads, paths, road cuts, eroded gullies, vacant lots, field edges, etc., provide favorable habitats for colonization by some species, such as *C. punctulata*. Similarly, the construction of farm ponds, lakes, and irrigation canals has probably aided species that live near water. On the other hand, increased use of insecticides, housing developments, polluted waterways, and the damming of rivers has undoubtedly adversely affected some species.

Man has also affected many saline habitats. Agricultural activities may lead to silting in of saline habitats in natural depressions. Schaffner (1898) said that a salt marsh in Republic County, Kansas, had suffered much in this manner already by 1897, being much smaller than it formerly was and having only several hundred acres without vegetation. Today, nearly the entire area is vegetated, some is being used for raising crops, and during the course of this study, a marshy area (Fig. 7) was drained and an unsuccessful attempt made to grow crops on it. As mentioned above, man may also create saline habitats by irrigation or drilling for oil. Fender (1945) reported finding one specimen of *C. cuprascens* (dead) and several of *C. punctulata* (three alive) in McMinnville, Oregon, in mail sacks from Council Bluffs, Iowa. These species are attracted to lights and must have fallen into the mail sacks at night. Thus, any species coming to lights may be transported considerable distances by man under favorable circumstances. Also, the larvae of any species could conceivably be transported by man in loads of soil.

THE LIFE CYCLE. Only a few of the world's species of cicindelids have had their life cycles worked out completely or even in part. Development takes one to several years, and some species do poorly under laboratory conditions, making them difficult to rear. Enock (1903) and Huie (1915) worked out the four-year cycle of *C. campestris*. Criddle (1910) studied the cycles of *C. limbata*, *C. limbalis*, *C. formosa*, and *C. lengi* in the field. Shelford (1908) worked out the cycles of *C. punctulata*, *C. purpurea*, *C. lepida*, *C. limbalis*, *C. formosa*, and *C. sexguttata* from laboratory and field observations and gave partial cycles for other species. Zikan (1929) reared many Brazilian species in several genera partly through their cycles. Shelford (1908, 1911) noted that temperature, moisture, climate, and food influence the length of

TABLE 11. Life cycles of *Cicindela* worked out by previous authors (Criddle, 1910; Shelford, 1908; Huie, 1915). Only one possible cycle is shown for each species; larval stages may be lengthened. The exact times of appearance of the stages varies geographically and from year to year. A=adult; O=oviposition; 1L, 2L, 3L=first, second, and third larval instars; P=pupa; ....=hibernation.

	1 year cycle (*C. punctulata*)	2 year cycle (*C. purpurea*)		2 year cycle (*C. lepida*)		3 year cycle (*C. lengi*)			4 year cycle (*C. campestris*)			
April	3L	A	3L	3L	2L	A	3L	3L	A	2L	3L?	3L
		0				0			0			
May		1L		P		1L						
	P								1L			
June								P				
	A	2L		A	3L							
	0			0		2L						
								A				P
July			P							3L?		
	1L	3L		1L								
									2L			
August	2L		A									A
				2L								
						3L						
Sept.	3L											
Oct.												

the different stages of the life cycle, particularly the larval stages; thus some of the species that Shelford studied at Chicago were found by Criddle to have longer life cycles in Manitoba, Canada. This, plus the facts that life cycles are long and adults oviposit for a number of weeks or months, often gives rise to great overlaps and a heterogeneity of cycles for a species. In general, two major types of life cycles can be delimited. In the first, adults emerge from the pupa in the fall, feed, hibernate, become active in the spring, and oviposit; variable larval stadia may produce a two to four year cycle. In the second type, adults emerge in the early summer and oviposit soon thereafter, dying off before winter; the total life cycle may last one to two years. The life cycles worked out by the above authors are shown diagrammatically in Table 11.

I succeeded in rearing only one individual of *C. togata* completely through its life cycle. Adults of *C. togata* were collected from Lincoln County, Kansas, on 7 September 1963, and kept in a laboratory terrarium. Several days later they began ovipositing. First instar larvae were first seen on 24 September 1963; on 28 January 1964, the larva that was eventually reared became a second instar larva; and on 20 April 1964, it became a third instar larva. The third instar burrow was last closed on 20 July 1965. An adult female, with elytra still soft, dug its way out of the soil on 6 September 1965, two years after the adults were collected. This evidence, plus observations on larvae in

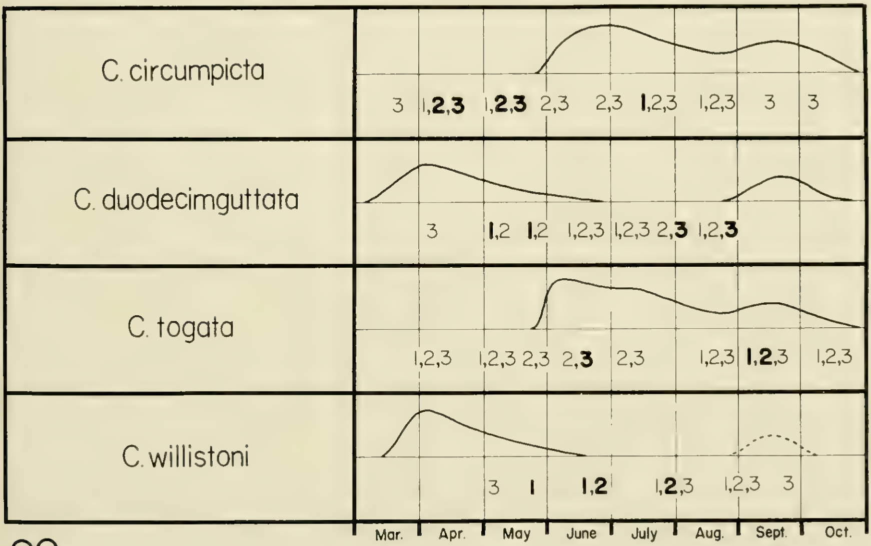

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Fig. 90. Temporal distribution of larvae of different instars (1=first, 2=second, 3=third) and adults (height of curve indicates relative abundance) of four species of saline habitats. A boldface number indicates that the instar was very abundant.

the field, leads to the conclusion that the life cycle takes two years (but may be lengthened to three), and is similar to that of *C. lepida* in Table 11. Larvae apparently hibernate in any of the three instars (Fig. 90).

In Figure 90 are shown times of the year that I have seen or collected larvae of different instars of four species. From these data and the times of adult activity, certain tentative conclusions can be drawn about the life cycles: *C. circumpicta* appears to have a life cycle similar to that of *C. togata*. *C. duodecimguttata* and *C. willistoni* probably have cycles similar to that of *C. purpurea* in Table 11; however, from the temporal distribution of larval instars, their cycles may only take one year.

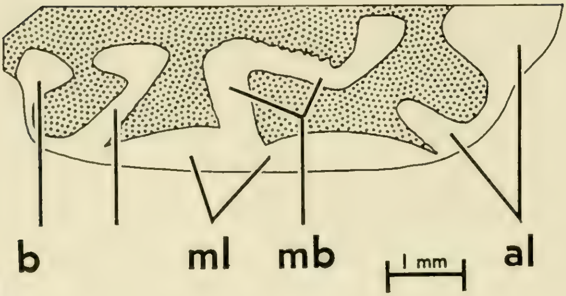
ZOOGEOGRAPHY OF *CICINDELA* OF SALINE HABITATS

Zoogeography is a very broad field of study, drawing its data from the disciplines of ecology, systematics, phylogeny, paleontology, paleoclimatology, physical geology, pedology, and geography. Zoogeography may be defined as the study of the distribution of animals in space and time, how and why this distribution came about, and prospects for future changes. Discussions of the principles and methods of zoogeography can be found in Darlington (1957) and Munroe (1963).

Many papers have appeared recently on the zoogeography of North American insects; e.g., Gressitt (1958), Howden (1963), Linsley (1939, 1958), Miskimen (1961), Rhen (1958), Ross (1953, 1958), and Ross and King (1952). The results of some of these can be applied to cicindelids. Works dealing with the zoogeography of cicindelids are fairly numerous. Horn (1908-1915) made speculations on the phylogeny and past dispersal of the family, but he was hampered by the relatively incomplete geological knowledge of the time. Rapp (1946) listed the distribution of the cicindelid genera on the seven major land masses of the world and hypothesized about their origin and dispersal. Crowson (1946) quickly criticized some of Rapp's conclusions. Kolbe (1935) expounded his theory of "morphological progressive animal dispersal," using the palearctic species *C. lunulata* as an example; the theory proposes that the most primitive forms occur at the place of origin and the most advanced at the periphery of the range. This is similar to the "age and area" hypothesis of J. C. Willis (see Darlington, 1957). Mandl (1954), studying the male genitalia of many of the cicindelid genera, hypothesized about their evolution and dispersal. Papp (1952), in a study of the male genitalia of 33 North American species of *Cicindela*, placed the species into groups of close relatives, noted the existence of close relatives in the palearctic region, and drew general conclusions about the evolution and dispersal of the North American cicindelid fauna. Schilder (1953b) subdivided the classical *Cicindela* into 18 genera and 29 subgenera, based at least partly on distribution, and speculated about their evolution and dispersal. Rivalier (1950, 1954, 1957, 1961, 1963) published a much more "natural" classification of the classical *Cicindela* (also subdividing it into genera) based primarily on the male genitalia. Ihering (1926) speculated about the dispersal of *Megacephala carolina*. Van Dyke (1929, 1939), in more general papers on North American Coleoptera, mentioned the faunal affinities of *Megacephala*, *Amblychila*, and *Omus*. Leconte (1875a, 1875b) proposed that the occurrence of *C. hirticollis* and *C. lepida* in similar habitats along the Atlantic coast and in the interior of North America could be explained by assuming that the inland populations are remnants of populations that lived on the shores of Cretaceous seas. Wickham (1904a, b) speculated on the evolution of *C. willistoni* and correlated its supposed evolution and dispersal with geological events. Shelford (1907) noted the preference of *C. sexguttata* for oak-hickory forests and predicted that as most forests of northeastern North America changed to a beech-maple climax (man eliminated), this species would be driven out of the area. Leng (1912) discussed factors controlling the distribution of the species of *Cicindela* of eastern North America: temperature, mountain barriers, local environment, behavior and adaptability of the species, accidents of climate and geological changes, and place of origin. Cazier (1948) treated the origin and dispersal of the cicindelid fauna of Baja California, Mexico, as it was known then. In a later publication (1954), he grouped the Mexican species of *Cicindela* according to their faunal relationships. Rumpp (1956, 1957, 1961) studied a number of species in the southwestern United States, including *C. willistoni*, *C. nevadica*, *C. fulgida*, *C. circumpicta*, and *C. togata*, and correlated their possible evolution and dispersal with geological events. Freitag (1965) postulated phylogenetic and zoogeographic schemes to explain the distribution, geographic variation, and systematics of nine North American species, particularly *C. duodecimguttata*, *C. oregona*, and *C. depressula*.

In this work, seven species were studied in detail zoogeographically: *C. circumpicta*, *C. cuprascens*, *C. fulgida*, *C. macra*, *C. nevadica*, *C. togata*, and *C. willistoni*. Brief mention will be made of other species. Each species will be discussed individually.

Methods. Data from several sources were used. The present known distribution of the species was determined by personal collecting and from records from the literature and museum collections. Geographic variation was studied statistically. Samples of specimens from various localities, assumed to have been collected at random, were measured. External morphological characters were used, such as lengths and widths of body parts, shapes of the white elytral maculation, and color. Males and females were studied separately. Size measurements were taken using an eyepiece micrometer in a binocular dissecting microscope and were later converted to millimeters.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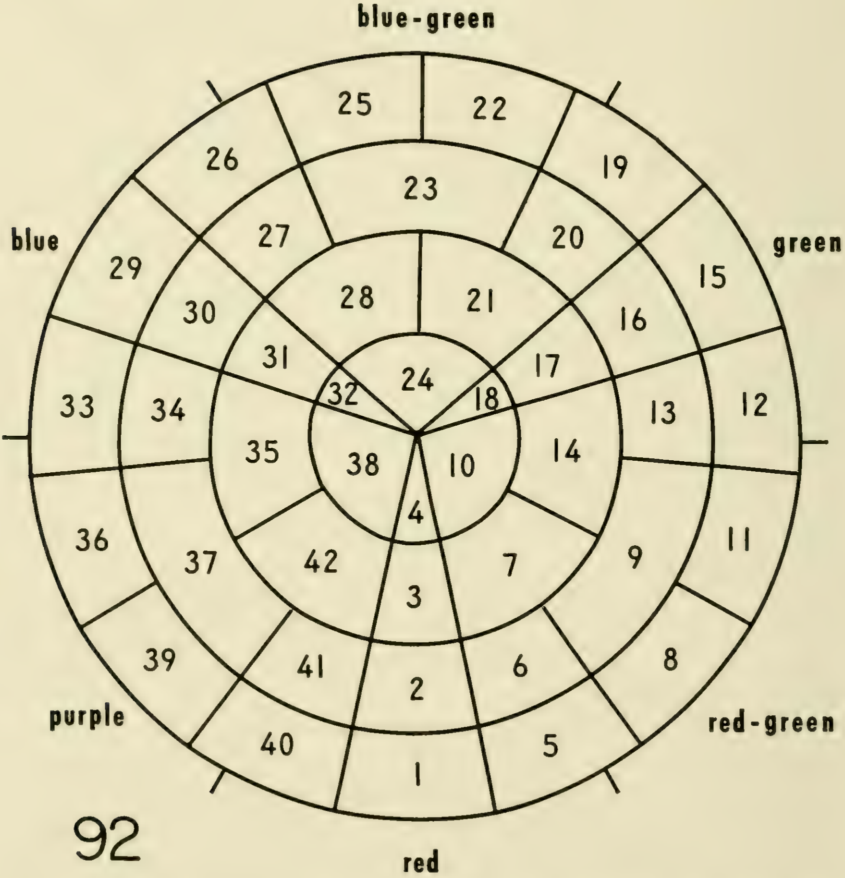
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FIG. 91. Left elytron of *C. cuprascens* (dorsal aspect), illustrating terminology of the maculation: al=apical lunule; b=basal dat, hl=humeral lunule, mb=middle band, ml=marginal line. FIG. 92. Color wheel used to study geographic variation of elytral color in five species of *Cicindela*. The brightest (most saturated) colors are around the rim; dark colors are toward the center, with black being at the center. The numbers are used for later reference. The marks outside the rim divide the wheel into six sectors for more simplified representations.

The possible shapes of the elytral maculation were subdivided into several arbitrary states, which were given numbers; specimens were then scored in decimal fractions of these states. The terminology used with the maculation is as follows (Fig. 91). The maculation is quite variable; however, a typical pattern consists of a humeral lunule (with or without a basal dot), middle band, and apical lunule. These markings may be connected at the margin by a marginal line. From this pattern the markings may be reduced to dots or complete absence, or they may be fused until the elytra are white or nearly so.

In the case of *C. togata*, variations of elytral color could be arranged in a linear series and represented by a scale of numbers; color was then treated as any other character. However, in the other species (except *C. fulgida*, for which color was not measured because of the temporal change of color noted in the section on adult post-emergence changes), the range of colors is more complex and had to be studied separately from the other characters. The possible colors, with but few exceptions, could be arranged in a color wheel (Fig. 92), with bright green, blue, and reddish at equidistant points at the edge, intermediate colors between them (blue-green, purple, red-green), and darker shades of the same colors toward the center (black being at the center). The color wheel was subdivided into 42 sections (numbers in Figure 92), and specimens were found which fit into all of them. The names of these colors, in the Ridgway (1912) and Inter-Society Color Council-National Bureau of Standards (Kelly and Judd, 1955) systems are given in Table 12. Specimens were examined against a white background with the naked eye, using overhead lighting from Sylvania cool white fluorescent bulbs. With the eye perpendicularly above the elytra, the position the specimen occupied on the color wheel was determined and a dot made on a data sheet with an outline of the wheel and its sections. Viewing such a sheet, with many dots representing a sample from a given locality, gives one an idea of the "color structure" of that population. For the purpose of comparing many populations on a map, a simplified, less detailed version of the color wheel was used because of space limitations on the maps.

The measurements, except those involving the color wheel, were analyzed, using an IBM 7040 computer, by the method of multivariate generalized discriminant functions. The computer program, available at the Computation Center of The University of Kansas, was written by Dr. F. James Rohlf, University of Kansas. It is called MULDIS, short for multigroup discriminant functions. The theory of generalized functions is explained in Jolicoeur (1959) and Seal (1964), where it is referred to as "canonical analysis." In brief, the method consists of a simultaneous analysis of the characters of specimens drawn from a number of localities. Any differences that exist among the groups of specimens can be displayed in the most efficient man-

TABLE 12. Color names of the sections of the color wheel (first column) in the Ridgway (1912) and Inter-Society Color Council—National Bureau of Standards systems. The names and numbers of the latter system often have greater latitude than those of the Ridgway system, accounting for duplication.

Section	Ridgway	ISCC-NBS
1	Brick red	strong reddish brown (40)
2	Hay's brown	moderate reddish brown (43)
3	Clove brown	dark grayish reddish brown (47)
4	Chaetura drab	brownish black (65)
5	Russet	strong brown (55)
6	Prout's brown	strong brown (55)
7	Natal brown	grayish brown (61)
8	Cinnamon brown	moderate brown (58)
9	Saccardo's olive	dark olive brown (96)
10	Dark olive	dark olive brown (96)
11	Dresden brown	light olive brown (94)
12	Forest green	deep yellow green (118)
13	Roman green	moderate olive green (125)
14	Dark dull yellow green	moderate olive green (125)
15	Cossack green	deep yellowish green (132)
16	Varley's green	dark yellowish green (137)
17	Danube green	dark green (146)
18	Dusky olive green	very dark yellowish green (138)
19	Meadow green	strong green (141)
20	Bottle green	deep green (142)
21	Duck green	very dark green (147)
22	Dark viridian green	strong green (141)
23	Invisible green	dark bluish green (165)
24	Dusky dull green	very dark bluish green (166)
25	Wall green	deep bluish green (161)
26	Myrtle green	deep bluish green (161)
27	Dusky green-blue (1)	dark greenish blue (174)
28	Dusky dull bluish green	very dark greenish blue (175)
29	Alizarine blue	deep blue (179)
30	Dusky orient blue	deep blue (179)
31	Dark delft blue	dark blue (183)
32	Bluish slate-black	dark blue (183)
33	Dark aniline blue	deep purplish blue (197)
34	Dull violet-black (3)	dark purplish blue (201)
35	Dull purplish black	dark violet (212)
36	Burnt lake	very deep purplish red (257)
37	Dusky auricula purple	very dark red (17)
38	Blackish violet-gray	blackish purple (230)
39	Vandyke red	dark red (16)
40	Madder brown	dark red (16)
41	Diamine brown	very deep red (14)
42	Dark mineral red	very deep red (14)

ner. One means for doing so is to transform the locality means into specially standardized units, so that the means of the localities can be plotted as points in an n-dimensional hyperspace, where n=number of characters, or number of localities −1, whichever is the smaller. The coordinate axes (generalized discriminant function) of these points are constructed so that the greatest amount of variance among localities (relative to that within localities) is explained by the first discriminant function, the next greatest amount by the second function, etc. Chi square tests are performed on each function; non-significant functions are ignored. A matrix of generalized distances is produced, giving the distance from the mean of one locality to that of any other; the greater the distance, the more different the specimens from the compared localities in the characters measured. One can also perform analyses of variance (anova) on each character with intermediate output of the program. A test is also made for homogeneity of the variances of the groups.

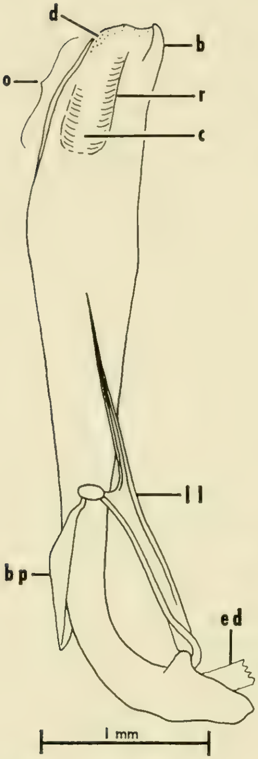
The significance of the differences in position of the means of the localities in n-dimensional hyperspace was tested using an unpublished method of Dr. K. R. Gabriel, called "likelihood ratio manova simultaneous testing procedure" (STP). Program 6, option D, available at the Computation Center of The University of Kansas, was used. In this method, the probability of making a type I error (that is, rejecting a true hypothesis) is known; a value of 5% was used. This is an experiment-wise error rate; a type I error will be made in 5% of the studies, or experiments. Another characteristic of this method is that if a certain set of means is found to be not significantly different, no subset within it will be significantly different.

Inferences about the phylogeny of the species studied were drawn from the literature, particularly Rivalier (1954), and from the results of this study. The grouping of species by Rivalier (1954) was used as a basis for the systematic arrangement of the North American fauna of *Cicindela*; however, it was found that certain minor corrections were necessary, on the basis of examination of the male genitalia of certain species. Mandl (1954) gives instructions for the preparation and observation of the male genitalia; however, in his method the inner sac is everted, making it difficult to see the interrelationships of the various internal parts. Freitag (1965) gave very brief instructions. The method I have developed is as follows:

1) If working with dried specimens, relax them for at least a day, or use a relaxing fluid.

2) Holding the beetle upside down, reach inside the genital opening with fine-pointed forceps and gently remove the aedeagus (it is best to use a low power dissecting microscope). Choosing specimens with the aedeagus partly extruded makes this easier. It may be necessary first to separate the aedeagus from the sclerites around the anus, to which it often adheres because of dried body fluids. Be careful that the curved proximal part does not break or that the basal piece and lateral lobes do not become separated.

3) Place the aedeagus in a 10% potassium hydroxide (KOH) solution for about 5-10 minutes to dissolve the tissue that usually adheres to the proximal part. Transfer it to a small Stender dish or microscope slide with a small amount of water and remove any remaining tissue with forceps. A weak acetic acid bath may be used to stop the action of the KOH.



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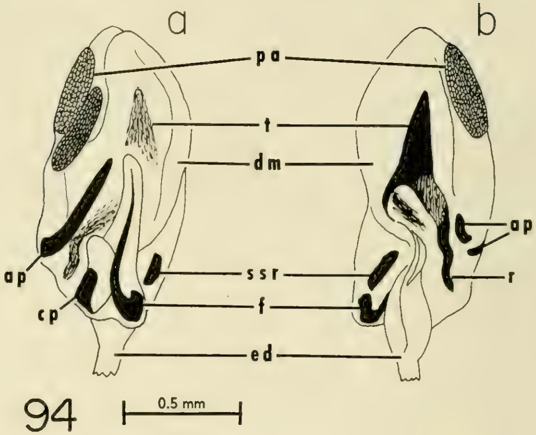

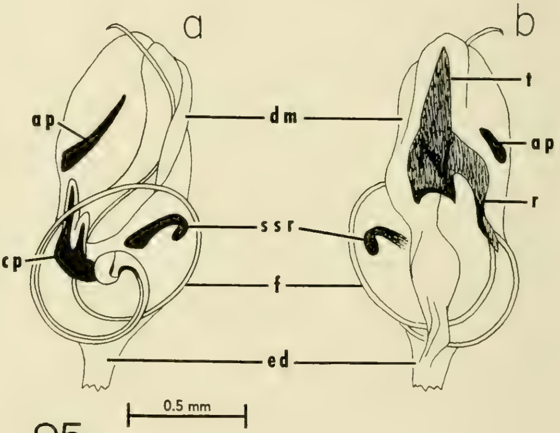

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FIG. 93. Aedeagus of *C. cuprascens* (Douglas County, Kansas), dorsal aspect. Abbreviations: b="beak," bp=basal piece, c=concavity, d=denticles, ed=ejaculatory duct, ll=lateral lobes (only one is drawn), o=orifice, r=ridge. FIG. 94. Inner sac of aedeagus of *C. fulgida* (Stafford County, Kansas); a, dorsal aspect; b, ventral aspect. Abbreviations: ap=arciform piece, cp=central plate (partly weakly sclerotized), dm=denticulate membrane, ed=ejaculatory duct, f=flagellum, pa=paired areas with large denticles, r=rod, ssr=small stiffening rod, t=tooth. FIG. 95. Inner sac of aedeagus of *C. cuprascens* (Douglas County, Kansas); a, dorsal aspect; b, ventral aspect. Abbreviations same as in Fig. 94.

4) Place the aedeagus on its "dorsal side" (as it lies at rest in the beetle) and make a drawing of it (see Fig. 93). This is best done with a camera lucida or ocular grid and graph paper. Note ridges, concavities, and denticles near the distal end. Also note the shape (curvature, thickness, etc.) of the entire aedeagus and of the heavily sclerotized part (often beak-shaped) at the apex, as well as the relative length of the lateral lobes. Sometimes a useful character is found by viewing the apex from the "side"; *i.e.,* from the direction of the orifice. Add a millimeter scale beside the drawing.

5) Slit the aedeagus longitudinally from about the middle to the apex. A scalpel or razor blade might work for this, but I used an insect pin with the point bent into a tiny hook, the pin

mounted in a wooden handle. Hold the proximal part of the aedeague with forceps and push the insect pin into it proximal to the inner sac to make a starting hole. Then pull the tool toward the apex, being careful not to poke it deep inside, using the hook to tear a slit. If the aedeagus is heavily sclerotized, this operation may be difficult.

6) Holding the proximal part of the aedeagus with forceps, reach inside the slit near the middle of the aedeagus with a fine teasing needle or another forceps, grasp the ejaculatory duct proximal to the inner sac, and gently pull the inner sac out of the slit. It will be connected to the aedeagus at the orifice by membranous cuticle; the membrane should be severed with a scalpel or teasing needle, being careful not to tear it where it continues over the inner sac.

7) Place the inner sac in a 10% KOH solution for 5-10 minutes, immerse it briefly in an acetic acid bath, remove it to a slide, and remove excess tissue with forceps, exposing the sclerotized membranes and pieces that compose the inner sac. The great complexity of these parts makes them difficult to draw. Make drawings from the dorsal and ventral aspects and any others that clarify the shapes and interrelationships of the parts. The sclerotized pieces are covered by membranes, often produced into complex folds; some parts of the membrane are transparent and some are covered by denticles of various sizes. The size and distribution of denticles is often an important character, usually more so among species groups than among closely related species. The sclerotized pieces show the most important characters; they vary widely in shape within the genus *Cicindela*, but they can usually be homologized from one species to another (see Rivalier, 1950-1963). Two examples, one of a more primitive species and one of a more advanced species, are shown in Figures 94 and 95. One can often see the parts of the inner sac more clearly if it is examined (by transmitted light) immersed in glycerin rather than water.

8) Keep all parts in glycerin in a corked microvial on the pin of the specimen.

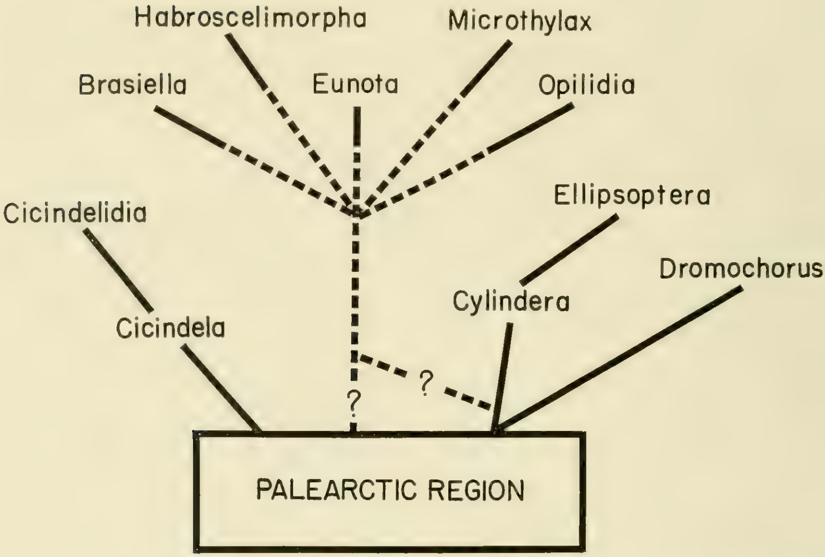
9) Examine the genitalia of at least several specimens of a form to determine the range of variation of the characters.

10) Be certain that the aedeagi and inner sacs are oriented the same way for drawings; a slight rotation can change the appearance of many parts.

PHYLOGENY

Unfortunately, few fossils of cicindelids are known. Horn (1906) discussed a *Megacephala* from the Baltic amber, which he said was conspecific with the modern American *M. carolina*, and hypothesized about how it happened to get there; however, Cockerell (1920) though that this specimen was a fake. Cockerell (1920) described a fossil, represented only by an elytron, from White River, Colorado (Green River age), as *Cicindelopsis eophilus*; however, as he pointed out, it does not have an inner apical elytral angle as do known cicindelids, and it may be from a cerambycid. G. Horn (1876) discussed two species of fossil *Cicindela* from a post-Pliocene cave at Port Kennedy, Pennsylvania. He said one is *C. haemorrhagica*, a species now restricted to the southwestern United States and northwestern Mexico; he did not name the other species. A close relative of *C. haemorrhagica*, *C. rufiventris* now occurs east of the Rockies; Horn could have misidentified the specimen.

Consequently, conclusions about the phylogeny of cicindelids must be drawn almost entirely from the present fauna. Earlier attempts to make phylogenies, e.g., Horn (1908-1915) and Schilder (1953b), were based on external morphological characters, particularly the elytral maculation in *Cicindela*. Mandl (1954) produced a much more satisfactory scheme (although fragmentary) for the family, using the male genitalia in addition to external characters. Papp (1952) arranged the species that she studied into


Habroscelimorpha
Microthylax
Brasiella
Eunota
Opilidia
Cicindelidia
Ellipsoptera
Dromochorus
Cylindera
Cicindela
?
?
PALEARCTIC REGION

Cicindela

C.hirticollis

C.duodecimguttata

C. repanda

C.fulgida

C.tranquebarica

Cicindelidia

C.willistoni

C.punctulata

C. schauppi

Habroscelimorpha

C.circumpicta

Eunota

C.togata

Ellipsoptera

C. nevadica

C.cuprascens

C.macra

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Fig. 96. Proposed scheme of evolution of the North American fauna of *Cicindela*. Names are the "genera" of Rivalier (1954). The species in this study are listed under their respective "genera" at the bottom.

groups progressing from phylogenetically old to young, as did Rivalier (1950-1963) in his more complete work. Rivalier made few statements about the actual phylogeny of his groups except for some remarks in his last paper (1963). From the meager comments of Mandl (1954), Papp (1952), and Rivalier (1963), and from the excellent systematic arrangement of Rivalier, it is possible to speculate on the phylogeny of the *Cicindela* of North America.

The family Cicindelidae and the genus *Cicindela* probably arose in Africa (Mandl, 1954). From there, secondary centers of evolution in the Old World tropics were colonized. Population of the New World by *Cicindela* probably occurred only from the north, via the Bering land bridge (although Mandl, 1954, thought that other genera dispersed to the New World at an earlier time via a southern land bridge).[4] Much radiation occurred in the New World, producing many indigenous groups ("genera" of Rivalier). A hypothetical scheme of evolution, using the names of Rivalier's "genera" is shown in Figure 96. At least two major ancestral stems crossed the Bering land bridge. One was *Cicindela* s. s., a group found throughout the Old World as well. This "genus" gave rise to *Cicindelidia*, which is restricted to the New World. The other major stem was *Cylindera*, a group also found throughout the Old World. It gave rise to *Ellipsoptera* and *Dromochorus*, which are restricted to the New World. The remaining five "genera" are an endemic, heterogeneous group whose origin is more uncertain. Probably at least some of them evolved from ancestors that crossed the Bering bridge; others may have split off the *Cylindera* stem.

Because of the paucity of cicindelid fossils, it is difficult to date the evolution of *Cicindela*. According to Carpenter (1953), the earliest known beetle fossils are from late Permian strata; cicindelids probably arose at about this time. The evolution of most of the cicindelid genera probably occurred during the Mesozoic. Horn (1908-1915) thought that the genus *Cicindela* became differentiated in the early Tertiary and that the ancestors of the American fauna crossed the Bering bridge in late Tertiary. Rumpp (1961) considered that the ancestors of *C. willistoni* had already reached North America by the beginning of the Tertiary, and that there has been little evolution of this species since Miocene time. Freitag (1965) thought that the ancestral stock of *Cicindela* s. s. may have been in existence in early Tertiary, and that living species may have evolved during late Tertiary or early Pleistocene. Thus it is possible that the evolution shown in Figure 96 took place in late Mesozoic and early Cenozoic times. The Bering land bridge was uplifted during most of this time, and the climate at that latitude was mild (Miskimen, 1961).

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[4] The question of land bridges is a touchy one. The presence of the Bering bridge during certain periods of geological time has been well established. Some early biogeographers were prone to "build" bridges where there was not the slightest shred of geological evidence to support them. For many years the trend has been away from this extreme. A related and even more volatile subject is continental drift. See Darlington (1957, 1965) and Simpson (1965) for recent discussions of these topics from the zoogeographical viewpoint.

SUBSPECIES

There has been a recent revival of interest in the question of whether subspecies have any reality in nature and, if so, whether they should be named in the formal system of Linnean nomenclature. Of particular importance is a series of papers in the journal, *Systematic Zoology.* Wilson and Brown (1953) condemned the arbitrariness and subjectivity of naming subspecies and pointed out several difficulties: 1) the tendency for independent characters to show independent geographic variation: 2) the ability of characters to appear in more than one geographic area, producing "polytopic" races; 3) the occurrence of microgeographic races; and 4) the necessary arbitrary lower limit of distinction of the subspecies. They further stated that subspecies as currently used are not units of evolution and that naming them conceals much variation. Other papers followed, supporting (Mayr, 1954; Parkes, 1955; Durrant, 1955; Smith and White, 1956) or refuting (Hubbell, 1959; Edwards, 1954; Peters et al., 1954; Gosline, 1954; Gillham, 1956; Hagmeier, 1958; Christiansen, 1958; Pimentel, 1959; Owen, 1963) the naming of subspecies.

My feelings on the subject, tempered by many of the above papers, as well as others, are as follows. Most of the difficulties mentioned by the opponents of subspecies are due to the extreme variability of animals. Populations of animals exist today in all stages of evolution, from a small, specifically distinct population inhabiting a single island, mountaintop, or valley, to widely distributed species, some of whose populations are not capable of interbreeding (see Mayr, 1963, for examples). In some species, one can find populations or groups of populations which are quite "distinct" in one or more characters from other populations of the species, while in other species this cannot be done. Thus, "distinct" intraspecific groups *may* exist within species. In the past, many such "distinct" groups (and some not so distinct) have been named as subspecies. At least some such groups (but by no means all) seem worthy of being named, if for no other reason than convenience in referring to them. In groups in which formal names have already been applied, one might just as well retain them. If no names exist, one may wish instead to use locality names or symbols to refer to them, as suggested by Hubbell (1954); although this may lead to confusion, as pointed out by Smith and White (1956). In some cases, some subspecies do appear to be units of evolution, as in geographically isolated populations, while in other cases they are not (at present), as in "distinct" groups among which gene flow occurs or is possible. There are all degrees of "distinctness" among intraspecific groups, making it impossible to set a nonarbitrary "lower limit" for subspecies. Statistical methods are useful in defining distinctness, but they can be misused. It is possible to find statistically "significant" differences between almost any two conspecific populations by using a large enough sample size, but these differences may have no biological significance. The many arbitrary limits, such as the "75% rule," the "84% rule," or the "95% rule," have been used with only limited success, and any one "rule" does not work well with all phyla of animals. Sokal and Rinkel (1963) pointed out the inadvisability of using such rules. I think that statistical methods, *plus* the opinion of a systematist familiar with the group of animals, are the only practical way to decide if a species should be subdivided and how, at our present state of knowledge. The recent development of methods such as numerical taxonomy may change this situation in the future.

Usually the naming of subspecies *does* conceal much variation; the study of species should not stop here. The variation of species, geographic and temporal, should be measured, studied, and shown by maps, graphs, etc. The use of a system of categories with a "higher degree of resolution," such as natio, subspecies, prospecies, species, and superspecies (see Schilder, 1953b, for an example using *Cicindela*), has not been popular, and in many cases the assignment of a form to a particular category is quite arbitrary. Subspecies are necessarily an oversimplification of the "true" situation. Nevertheless, if subspecies reflect to some degree the actual pattern of variation, as well as being convenient "handles" for reference, their value seems sufficient to justify their recognition.

In the genus *Cicindela* many of the species exhibit pronounced geographic variation, particularly of color and elytral maculation. For example, of the approximately 80 species occurring in North America north of Mexico, about 45 exhibit pronounced variation. Past workers have named many forms, which are now recognized as subspecies, varieties, intergrades, melanic forms, seasonal forms, and individual variants. Often, forms were described before the total distribution of variation of the species was known, or were described from inadequate series. Thus, one task of the present-day student of North American cicindelids is to make thorough studies of the variation of species and decide whether subspecies or formerly unrecognized sibling species exist (and should be named) within what have been called species. This will be done with the seven species studied thoroughly here.

Being familiar with the variation of many of the Cicindelas of North America, I think a subspecies in this group should have the following characteristics: (1) occupy a well defined geographic area or ecological habitat, separate from that of other subspecies within the same species (zones of intergradation may occur between neighboring subspecies); (2) exhibit a

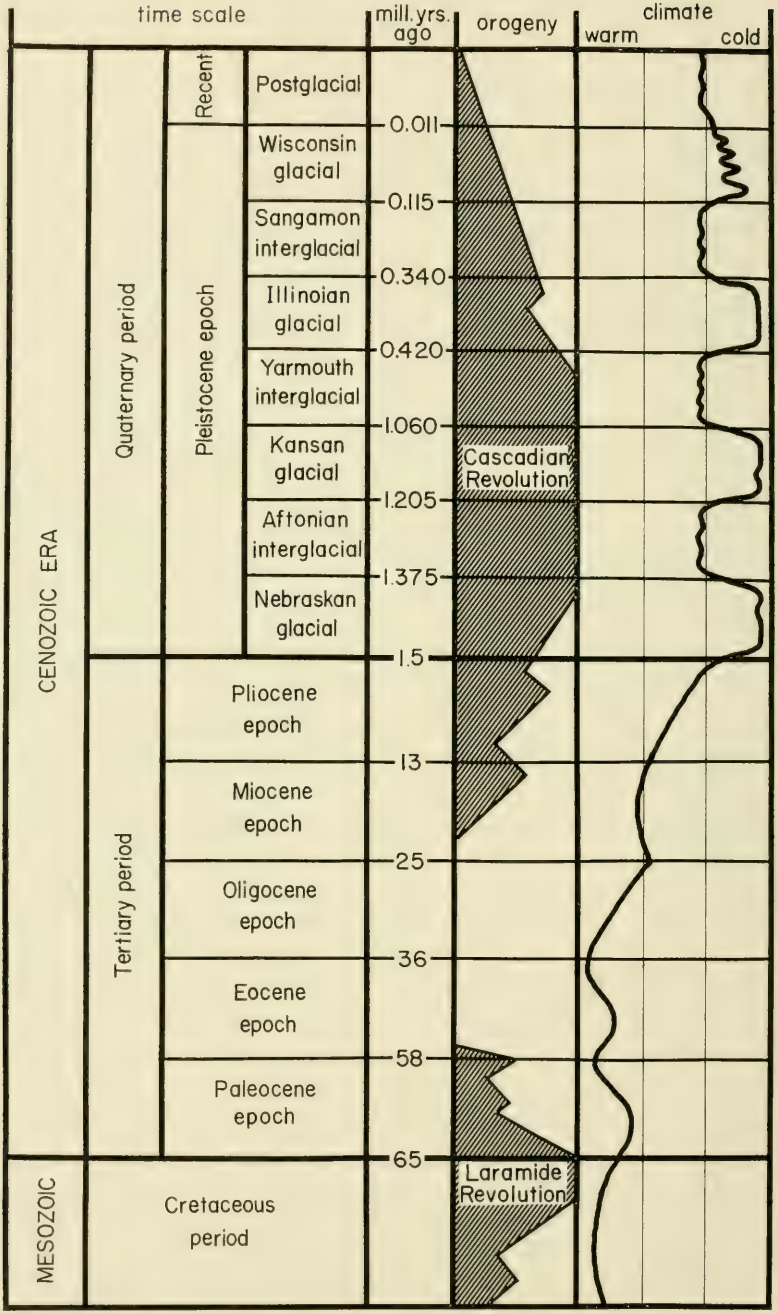

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FIG. 97. Partial geological time scale and important events in North America. From Dunbar (1960) and Dorf (1960).

relatively uniform expression of characters within itself; (3) be readily separable from other subspecies by one and preferably more characters.

These characteristics are obviously vague and contain no minimum degree of difference for a form to be a subspecies. I think each case should be considered individually (but comparison with the variational pattern of other species may be helpful) because cases will no doubt be found in which two forms may be "on the verge" of becoming species. Any clues on the past distribution or dispersal of the species (e.g., ancient river courses for fluvial species) should be considered. The problem is further complicated by the existence in many species of some forms which are much more distinct (and obviously subspecies) than others. Clearly there must be some subjectivity in the naming of subspecies.

CENOZOIC GEOLOGY AND CLIMATE

Before discussing the zoogeography of individual species, it would be well to review the major geological changes and paleoclimates that occurred in North America during the Cenozoic Era, when most of the evolution and dispersal of the species in this study probably took place. This amount is drawn from a number of sources. See Miller (1952), Dunbar (1960), King (1958), MacGinitie (1958), Dorf (1960), Braun (1947, 1955), Axlerod (1950), Chaney (1947), Deevey (1949), Dillon (1956), Thornbury (1965), and Wright and Frey (1965) for more details. See also Figure 97 for a geologic time scale.

The Cenozoic Era was marked by two great periods of orogeny, or mountain building activity. Beginning in the Cretaceous and continuing until early Eocene, the Laramide Revolution thrust up the initial Rocky Mountains in western North America. These mountains were eroded almost to a level peneplain by Miocene times, when the Cascadian or Cordilleran Revolution began, uplifting the western mountains again to their present height. During the Laramide Revolution, numerous basins were formed in the western United States, and in the Miocene, the Basin and Range province, which had a high mountainous surface and exterior drainage, began to assume its present character. As the initial Rockies were eroded, these basins were filled and sediment was carried eastward across the interior of the continent.

During most of the Tertiary, eastern North America, from central Alabama to the Gulf of St. Lawrence, which had been uplifted slightly at the close of the Cretaceous, was eroded to a nearly flat peneplain. Near the end of the Tertiary the area was again uplifted unevenly, and erosion increased to produce the present topography. The Atlantic and Gulf coastal plains were partially submerged from Paleocene to Oligocene or even Pliocene in some areas, but in general they gradually grew in size throughout the

Tertiary. A remnant from Cretaceous times, the Mississippi embayment, an arm of the Gulf of Mexico extending up the present Mississippi valley to southern Illinois, was gradually filled with sediment in the late Tertiary.

In late Cretaceous times, the climate was mild throughout most of the earth. Plants such as figs, cycads, palms, and tree ferns grew as far north as central Greenland and Alaska. The climate was nevertheless zoned as it is today. The tropics extended northward to about 35 or 40° latitude. From here to about 55 or 60° N latitude, subtropical conditions prevailed. Temperate climates extended to about 70° N latitude, north of which subarctic conditions occurred.

Conditions during the early Tertiary did not change greatly. The western mountains were mostly of moderate elevation and did not affect climate appreciably. By mid-Eocene times there were at least three botanical provinces in North America. In the far western states a subtropical forest extended along the coast and inland as far as northwestern Wyoming (Neotropical-Tertiary flora). The low-lying shores of the Mississippi embayment were occupied by a tropical flora (Wilcox flora). Far to the north extended the hardwood deciduous and coniferous Arcto-Tertiary forests. Arid conditions began to appear locally in northwestern Colorado and southern Wyoming, although the modern desert vegetation had not yet evolved.

Beginning in the Oligocene, a trend of gradual cooling and drying climates began. The northern Arcto-Tertiary forests began to move southward through the western United States, displacing tropical and subtropical floras. A climatic barrier of reduced rainfall prevented any of these species from entering the Appalachian region or Mexico. The Miocene saw the evolution of the semiarid Madro-Tertiary flora in northern Mexico and southern California, while the Arcto-Tertiary flora became more restricted. An ecotone existed between them in southern Nevada. The Arcto-Tertiary flora evidently still had a dispersal path to the eastern United States through southern Canada. In the vicinity of Washington, D.C., a low coast existed, lined with cypress swamps and coastal sand dunes.

Beginning in mid-Miocene and especially during the Pliocene, the present grasslands developed in the western two-thirds of the continent, replacing subtropical scrub in the region between the Rocky Mountains and the Mississippi embayment. Farther east, the mixed deciduous forests retreated and were replaced by oak forests. Temperatures cooled, rainfall decreased, and seasonal fluctuations increased, until in late Pliocene conditions were essentially like they are today. The uplift of the western mountains and their resultant rain-shadow effect played a major role in the development of the prairies and deserts.

The climatic changes begun in the Tertiary culminated in the Pleistocene epoch. A cyclic climatic pattern developed, producing alternating glacial and nonglacial stages. Four major glacial periods (the Wisconsin is subdivided by some authors) alternated with interglacials (Fig. 97). During the glacials, huge masses of ice moved southward, and mountain glaciers developed and increased in size. South of the glaciers rainfall increased, creating many large lakes in the Great Basin (the glacials are also called pluvial periods). The continental glaciers pushed farthest south in the central United States, reaching the present Ohio River and northeastern Kansas. Climatic zones were greatly compressed near the glaciers and shifted south (or down mountains) a certain amount; exactly how far is a point of disagreement among authors. Early authors thought that glaciation pushed the flora and fauna far south into Mexico and Central America. More recent authors, e.g., Dillon (1956), Dorf (1960), felt that climatic zones were more compressed than shifted south, and that the Gulf coast was still subtropical. Graham (1964) thought the glaciers had little effect on the biota of the southeastern United States. Probably a narrow band of tundra existed immediately south of the glaciers, followed by bands of subarctic, temperate, and subtropical climate as one moved south. Ranges of mountains in the West would produce a more complicated pattern, greatly influenced by elevation. During the interglacial periods the climatic zones and biota moved northward (and up mountains) to or slightly beyond their present positions.

The glaciers had profound effects on the sea level. During glacials the sea level was about 100 meters lower than at present, exposing much of the continental shelves and allowing the Bering land bridge to connect Eurasia and North America. The glaciers also had great effects on many North American streams. As mentioned, during glacials rainfall increased near the glaciers. Many streams in the Great Basin which now are intermittent or dry could have been important in the dispersal of certain organisms. Also, many changes in the courses of streams occurred and may have affected the distribution of organisms.

At present we appear to be in an interglacial period, with the next glacial period predicted to occur in 10,000 to 15,000 years. During the last several hundred years the mean world temperatures have been rising, glaciers are melting, and northward movements of animals such as seals, codfish, and armadillos have been noted.

MINOR SPECIES

Miscellaneous distribution records on the species not studied intensely follow.

C. duodecimguttata

The systematics and zoogeography of this species were studied thoroughly by Freitag (1965). Besides what has been mentioned in earlier sections, I offer the following personal collection records:

KANSAS: Republic Co., ½ mi. east, 1 mi. south of Talmo, 6 Sept. 1963; 4 mi. northwest of Jamestown, 14 Sept. 1964; Lincoln Co., 3 mi. west, 2 mi. south of Barnard, 14 Apr., 7 Sept. 1963; Greenwood Co., 2 mi. west, 1 mi. north of Severy, 11 May 1963; 1.5 mi. west of Severy, 11 May 1963; Wilson Co., west edge of Fredonia (city park), 11 May 1963, 6 Apr., 20 June 1964; Woodson Co., 5 mi. north of Yates Center, 20 Apr., 10 May 1963, 6 Apr. 1964; Butler Co., west edge of El Dorado, 11 July, 9 Sept. 1964, 21 May 1965; Sumner Co., 4.5 mi. west of Geuda Springs, 21 Apr. 1963; MISSOURI: Howard Co., 1 mi. north of Rocheport, 24 June 1963; TEXAS: Rockwall Co., 2.5 mi. southwest of Royse City, 30 June 1965.

C. hirticollis

This species is currently being studied by Dr. R. C. Graves. Collection records from saline habitats of the central United States are as follows:

KANSAS: Lincoln Co., 11 mi. north, ½ mi. east of Lincoln, 14 June 1964; Stafford Co., 11 mi. northeast of Hudson, 7 Apr. 1965; Barber Co., 3 mi. southeast of Hazelton, 27 Aug. 1963; 17.5 mi. west, 4 mi. north of Hardtner, 30 Aug. 1963; Comanche Co., 12 mi. south of Protection, 29 Aug. 1963; OKLAHOMA: Hughes Co., 5 mi. north of Holdenville, 29 June 1965; Seminole Co., 12.5 mi. south of Seminole, 29 June 1965; McClain Co., south edge of Purcell, 1 July 1965; Logan Co., 3 mi. north of Guthrie, 1 July 1965; Creek Co., just north of Oilton, 19 Aug. 1964; Woods Co., 2.5 mi. southwest of Plainview, 3 June 1963; Woods-Harper Co. line, 6 mi. west-northwest of Plainview, 29 Aug. 1963; Grant Co., just east of Pondcreek, 10 Sept. 1964; Major Co., 2 mi. northeast of Orienta, 12 July 1964; Kingfisher Co., 2 mi. south of Dover, 10 Sept. 1964; Blaine Co., 7 mi. south of Okeene, 21 June, 10 Sept. 1964; TEXAS: Cooke Co., 1 mi. northeast of Rosston, 30 June 1965.

Populations of *C. hirticollis* in the central United States have traditionally been called the subspecies *C. h. ponderosa* Thomson, but this is not satisfactory because the type locality is Veracruz, Mexico, and specimens from the two areas are not the same. The study by Graves should clarify the matter.

C. punctulata

This is an extremely common species which is found from central Mexico to southern Canada, and from Utah and Arizona to Maine and Florida. Most of the Mexican populations belong to the subspecies *C. p. catharinae* Chevrolat (see Cazier, 1954). In the southwestern United States is found the bright green, blue, or purple form, *C. p. chihuahuae* Bates. In general, the form east of the Rocky Mountains is the dark *C. p. punctulata* Olivier, although populations from Colorado, northeastern Utah, western Kansas, the Oklahoma and Texas panhandles, and eastern New Mexico seem to be intergrades between *C. p. punctulata* and *C. p. chihuahuae*. Collection records from this study (county only) are as follows:

NEBRASKA: Lancaster, Saunders; KANSAS: Republic, Lincoln, Mitchell, Russell, Neosho, Greenwood, Woodson, Wilson, Montgomery, Butler, Sedgwick, Sumner, Stafford, Kingman, Kiowa, Barber, Comanche, Clark; MISSOURI: Howard; OKLAHOMA: Seminole, Logan, Creek, Osage-Pawnee Co. line, Woods, Alfalfa, Grant, Major, Garfield, Blaine, Kingfisher, Beckham, Harmon; TEXAS: Fannin, Hunt, Collin, Montague.

C. repanda

This widely distributed species occurs from Texas (and possibly Mexico, near El Paso, Texas) to about 58° N latitude in Canada, and from Washington to Nova Scotia (it is absent from the Great Basin but occurs on the Colorado Plateau). It exhibits little geographic variation. Populations in Nova Scotia and vicinity have reduced elytral maculation and have been designated *C. r. novascotiae* Vaurie. Individuals in east central Utah are small, with expanded elytral maculation, and are called *C. r. tanneri* Knaus. The remaining populations may be called *C. r. repanda* Dejean, although other names have been applied to certain forms. Collection records from saline habitats are as follows (county only):

NEBRASKA: Saunders; KANSAS: Republic, Lincoln, Russell, Wilson, Sumner, Kiowa, Barber, Comanche; MISSOURI: Howard; OKLAHOMA: Hughes, Seminole, McClain, Creek, Woods, Alfalfa, Grant, Garfield, Kingfisher; TEXAS: Cooke.

C. schauppi

This is a species of southern distribution which reaches its northern limit in the central United States. North of Texas it is uncommon. I have collected it only once, in Okfuskee Co., Oklahoma, just northwest of Pharoah (19 Aug. 1964), on a bare, slightly saline area caused by oil drilling. This and other localities from the literature and museum collections are shown in Figure 98. *C. schauppi* exhibits some variation, specimens from northern localities having a longer, thinner, and more oblique middle band than do those from

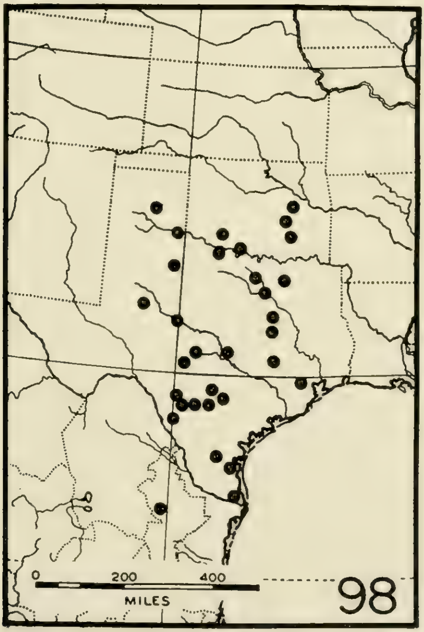


FIG. 98. Known distribution of *C. schauppi*. FIG. 99. Known distribution of *C. circumpicta*; triangle=*C. c. circumpicta*, dot=*C. c. johnsoni*.

southern and western Texas, but so few large series of specimens exist that a statistical study of variation would not be very meaningful. Further study may show that subspecies are worthwhile naming. Locality records are as follows (county or state only):

OKLAHOMA: Okfuskee, Coal, Hughes, Jefferson, Comanche; TEXAS: Wichita, Hunt, Wilson, Atacosa, Brazos, Frio, Uvalde, Limestone, King, Dimmet, Cameron, Kleberg, Burnet, Dallas, Childress, Kimble, Zavala, Bexar, Mason, Runnels, Duval, Denton, Nevarro, Nueces, Howard, Carson, Harris; MEXICO: Nuevo Leon. Doubtful locality: KANSAS: Parsons, Labette Co.; this specimen more resembles those from southern Texas than those from Oklahoma.

C. tranquebarica

This is a very widely distributed species, found from the Pacific coast to Newfoundland and from the Gulf coast to 60° N latitude in Canada. Populations east of the Rocky Mountains exhibit little variation and are called *C. t. tranquebarica* Herbst. West of the Rocky Mountains there occurs a multitude of subspecies (at least 11), which have been insufficiently studied. Collection records for saline habitats are the following:

KANSAS: Republic Co., 4 mi. west, 1 mi. south of Kackley, 6 Sept. 1963; Stafford Co., 11 mi. northeast of Hudson, 9 Apr. 1964; OKLAHOMA: Woods Co., 2.5 mi. southwest of Plainview, 3 June 1963.

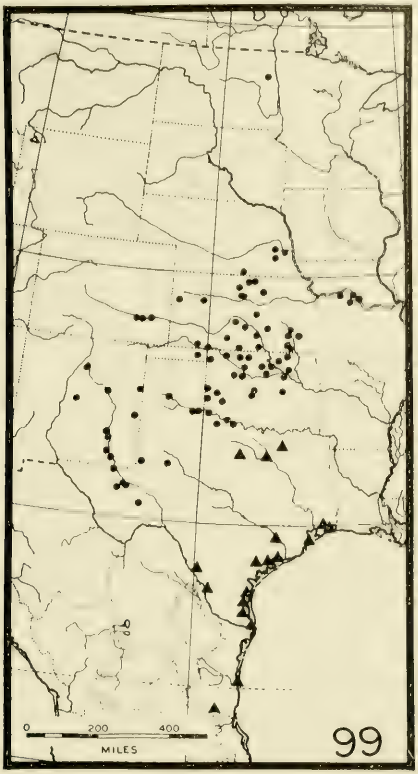
MAJOR SPECIES

In this section, those species that were studied most thoroughly are discussed. For each species, I will consider: (1) present distribution (as well as it is known), geographic variation, and the presence or absence of subspecies; (2) why it is found where it is, including adaptations, evolution, and dispersal.

C. circumpicta

This species is of primarily southern distribution, being most common along the western Gulf coast, along the Pecos River, and in Oklahoma and Kansas. It also occurs in Colorado, Missouri, Nebraska, and has recently been collected in eastern North Dakota (Fig. 99). *Doubtful records* exist (Lyons, Cook Co., Illinois; Riley Co., Kansas; Patagonia, Santa Cruz Co., Arizona); and the town of Manzenda, Colorado (=Manzanola, Otero Co. ?) could not be located. Locality records are as follows (county or state only):

NORTH DAKOTA: Grand Forks; NEBRASKA: Lancaster, Nuckolls, Saunders; MISSOURI: Boone, Howard, Saline; KANSAS: Barber, Butler, Clark, Clay, Gove, Kiowa, Lincoln, McPherson, Meade, Mitchell, Montgomery, Neosho, Reno, Republic, Sedgwick, Seward, Stafford, Sumner, Wallace, Wilson, Woodson; COLORADO: Bent, Otero; OKLAHOMA: Alfalfa, Beaver, Beckham, Blaine, Cleveland, Creek, Garfield, Grant, Harmon, Harper, Jackson, Kingfisher, McClain, Noble, Okfuskee, Oklahoma, Osage, Pawnee, Payne, Tillman, Tulsa, Washington, Woods; NEW MEXICO: Chaves, Eddy, Guadalupe, Quay, Roosevelt, Santa Fe, Torrance; TEXAS: Andrews, Cameron, Childress, Colorado, Dallas, Dimmet, Galveston, Goliad, Hall, Hardeman, Howard, Hunt, Jackson, Jefferson, Kenedy, Kleberg, Loving, Nueces, Palo Pinto, Pecos, Randall, Reeves, Victoria, Webb, Wichita, Wilbarger; TAMAULIPAS.

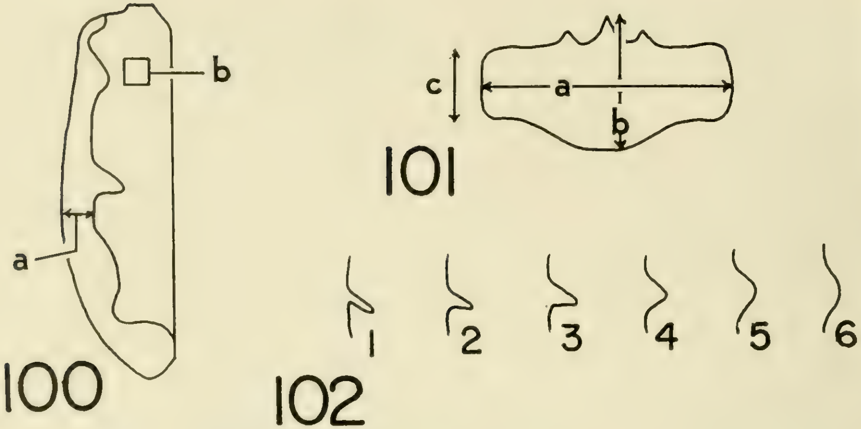


The described forms within this species are the following:

Cicindela circumpicta LaFerté, 1841. Type locality: Texas.
Cicindela collaris LaFerté, 1841. Type locality: Texas.
Cicindela Johnsonii Fitch, 1856. Type locality: prairies west of Arkansas.
Cicindela circumpicta ambiens Casey, 1913. Type locality: Kansas.
Cicindela circumpicta inspiciens Casey, 1913. Type locality: Point Isabel, Texas.
Cicindela circumpicta salinae Vaurie, 1951. Type locality: Lincoln, Lancaster County, Nebraska.

In recent years, three subspecies have been recognized: *C. c. circumpicta*, the dark, mostly coastal form; *C. c. johnsoni*, the bright inland form occurring in three color phases; and *C. c. salinae*, the dull reddish or brown form from the Lincoln, Nebraska, vicinity.

In the study of geographic variation, the following characters were measured: (1) width of head at widest point (the eyes); (2) width of pronotum at widest point; (3) width of left elytron at widest point when viewed from directly above, not at an oblique lateral angle; (4) width of the white elytral maculation at a specified place (Fig. 100a); (5) length of left elytron from the level of the anterior end of the scutellum to the most apical part; (6) num-



FIGS. 100-102. Illustration of certain characters measured on *C. circumpicta*; FIG. 100, a=width of elytral maculation, b=number of punctures in 0.45 mm^2 area at this position; FIG. 101, a=width of labrum, b=length of labrum, c=length of labrum at one lateral edge; FIG. 102, arbitrary units for shapes of the middle bands.

ber of punctures in a 0.45 mm^2 square on a specified part of the left elytron (Fig. 100b); (7) width of labrum at widest point (Fig. 101a); (8) length of labrum at midline, including tooth (Fig. 101b); (9) length of labrum at one lateral edge (Fig. 101c); (10) length of hind tarsus, excluding claws; (11) length of hind tibia; (12) shape of middle band in arbitrary units (Fig. 102); (13) color of elytra, using color wheel.

Specimens from 23 localities were measured for characters 1-12; the localities and sample sizes are given in Table 13. Specimens from 21 of these localities and ten additional localities were included in the color analysis (Table 13). When possible, samples of 20 specimens of each sex were used, but in a few cases only small samples were available or specimens from two or more nearby localities were lumped into a larger sample. The values obtained from these less desirable samples are thus less reliable than those of samples from one locality.

The means for the characters and localities are given in Tables 14 and 15. Analyses of variance of the individual characters showed that there are significant differences ($p < 0.01$) among the means of all characters for both sexes. Pooled within-locality variance-covariance matrices are given in Tables 16 and 17. The sums of the among-locality variance components are 100.907 for males and 127.336 for females. The first six components for males and the first seven for females are highly significant ($p < 0.01$), and the seventh is significant at the 5% level for males; however, the first three functions account for 77.67% of the variance (among localities relative to that within) in males and 78.19% in females. The first six functions account for 93.96%

TABLE 13. Localities and samples sizes of the specimens of *C. circumpicta* measured.

	Locality	N	
		♂	♀
1.	NORTH DAKOTA, Grand Forks Co., 1.5 mi. n.e. of Emerado	20	20
2.	NEBRASKA, Lancaster Co., Lincoln (west edge)	20	20
3.	KANSAS, Republic Co., ½ mi. e., 1 s. of Talmo	9	14
4.	KANSAS, Republic Co., 4 mi. w., 1 s. of Kackley	20	15
5.	KANSAS, Lincoln Co., 3 mi. w., 2 s. of Barnard	20	20
6.	KANSAS, Stafford Co., 11 mi. n.e. of Hudson	20	20
7.	MISSOURI, Howard Co., 1 mi. n., 2 w. of Boonesboro	20	20
8.	KANSAS, Montgomery Co., 3 mi. s. of Elk City	20	20
9.	OKLAHOMA, Creek Co., 3 mi. s.e. of Sapulpa	20	19
10.	OKLAHOMA, Alfalfa Co., 3 mi. e. of Cherokee	20	20
11.	OKLAHOMA, Woods Co., 2.5 mi. s.w. of Plainview	20	20
12.	KANSAS, Clark Co., Englewood	20	20
13.	OKLAHOMA, Blaine Co., 7 mi. s. of Okeene	17	10
14.	OKLAHOMA, Beckham Co., 6 mi. w. of Mayfield	14	11
15.	OKLAHOMA, Jackson Co., 3.5 mi. s. of Eldorado	20	17
16.	NEW MEXICO, Chaves Co., 10 mi. e., 5 s. of Roswell	20	20
17.	NEW MEXICO, Eddy Co., 6 mi. e., 2 n. of Loving	11	8
18.	TEXAS, Reeves Co., vicinity of Pecos, Lake Balmorhea, Toyah; Pecos, Co., Ft. Stockton; Loving Co.	13	20
19.	TEXAS, Webb Co., Laredo; Dimmet Co., Carrizo Springs	6	6
20.	TEXAS, Cameron Co., Port Isabel, Boca Chica, Brownsville	12	19
21.	TEXAS, Kleberg Co., Riviera Beach	20	20
22.	TEXAS, Galveston Co., Seabrook, Galveston, Dickinson*	1	2
23.	TEXAS, Dallas Co., Dallas; Hunt Co., Wolfe City*	2	3
Localities included in color analysis only:			
24.	KANSAS, Lincoln Co., 11 mi. n. of Lincoln		
25.	KANSAS, Wilson Co., 1 mi. n., ½ w. of Fredonia		
26.	KANSAS, Neosho Co., 2 mi. n., ½ e. of Chanute		
27.	KANSAS, Sumner Co., just n. of Geuda Springs		
28.	KANSAS, Barber Co., 3 mi. s.e. of Hazelton		
29.	KANSAS, Kiowa Co., 1 mi. n. of Belvidere		
30.	OKLAHOMA, Tulsa Co., 1.5 mi. s. of Skiatook		
31.	OKLAHOMA, Garfield Co., ½ mi. n.w. of Drummond		
32.	OKLAHOMA, Beckham Co., 3 mi. s. of Carter		
33.	TEXAS, Wichita Co., 2 mi. n.e. of Burkburnett		
34.	TEXAS, Hardin Co., Sour Lake		

* Excluded from color analysis.

TABLE 14. Means of 23 localities (see Table 13) and 12 characters for males of *C. circumpicta.* Values for characters 1-5, 7-11 are in mm.

	Character											
Locality	1	2	3	4	5	6	7	8	9	10	11	12
1	3.36	2.57	2.21	0.61	8.16	30.4	1.60	0.75	0.47	4.91	4.86	4.18
2	3.33	2.54	2.15	0.41	7.97	34.4	1.54	0.71	0.44	4.68	4.71	2.96
3	3.46	2.73	2.25	0.44	8.51	33.3	1.62	0.75	0.46	5.14	4.99	3.31
4	3.53	2.81	2.34	0.46	8.62	30.9	1.65	0.79	0.48	5.25	5.23	2.85
5	3.26	2.56	2.13	0.41	7.88	33.8	1.51	0.73	0.44	4.77	4.76	3.00
6	3.53	2.76	2.33	0.52	8.54	28.8	1.63	0.80	0.48	5.15	5.21	3.45
7	3.51	2.73	2.29	0.41	8.42	29.5	1.62	0.79	0.50	4.89	4.93	3.13
8	3.50	2.72	2.31	0.44	8.52	29.6	1.60	0.76	0.47	4.95	5.01	3.01
9	3.39	2.59	2.20	0.50	8.09	30.8	1.55	0.76	0.46	4.81	4.82	3.27
10	3.47	2.69	2.31	0.46	8.30	29.7	1.59	0.77	0.48	4.95	5.04	3.46
11	3.52	2.72	2.34	0.50	8.51	28.8	1.61	0.79	0.49	5.13	5.18	3.30
12	3.25	2.54	2.19	0.49	7.90	31.8	1.49	0.71	0.45	4.90	4.85	3.89
13	3.40	2.47	2.20	0.43	7.91	29.0	1.49	0.72	0.45	4.73	4.79	3.06
14	3.45	2.63	2.30	0.47	8.32	31.1	1.60	0.76	0.48	5.12	5.12	3.11
15	3.61	2.78	2.43	0.54	8.81	29.1	1.65	0.81	0.51	5.18	5.22	3.13
16	3.47	2.67	2.30	0.57	8.39	32.3	1.60	0.77	0.49	5.42	5.39	3.76
17	3.31	2.48	2.16	0.57	7.89	34.6	1.49	0.72	0.46	5.04	5.01	4.29
18	3.54	2.73	2.35	0.64	8.55	29.6	1.63	0.80	0.50	5.42	5.35	3.98
19	3.45	2.50	2.21	0.42	8.19	29.0	1.53	0.83	0.48	5.18	5.17	1.93
20	3.79	2.87	2.38	0.40	8.73	22.0	1.70	0.88	0.52	5.62	5.58	1.64
21	3.92	2.97	2.48	0.42	8.99	22.4	1.78	0.89	0.54	5.88	5.85	1.38
22	3.17	2.25	2.05	0.46	7.17	33.0	1.36	0.69	0.39	4.61	4.56	1.20
23	3.33	2.59	2.10	0.38	8.12	29.0	1.55	0.82	0.46	4.99	4.89	1.95

Table 15. Means of 23 localities (see Table 13) and 12 characters for females of *C. circumpicta*. Values for characters 1-5, 7-11 are in mm.

	Character											
Locality	1	2	3	4	5	6	7	8	9	10	11	12
1	3.66	2.83	2.44	0.55	8.62	27.7	1.71	0.80	0.47	4.28	4.73	4.02
2	3.72	2.90	2.44	0.47	8.72	31.1	1.69	0.80	0.47	4.37	4.79	2.98
3	3.72	2.91	2.49	0.47	8.91	31.1	1.70	0.79	0.48	4.49	4.88	2.89
4	3.75	3.01	2.55	0.49	9.04	28.6	1.74	0.82	0.48	4.51	4.87	2.97
5	3.51	2.73	2.34	0.41	8.41	30.1	1.61	0.75	0.46	4.28	4.66	3.09
6	3.85	3.02	2.59	0.48	9.12	26.5	1.75	0.85	0.52	4.58	5.06	3.06
7	3.70	2.84	2.41	0.40	8.74	28.1	1.70	0.82	0.51	4.26	4.75	3.13
8	3.75	2.90	2.47	0.45	8.88	27.2	1.71	0.80	0.49	4.41	4.85	3.16
9	3.68	2.82	2.40	0.51	8.70	28.5	1.65	0.81	0.47	4.32	4.66	3.11
10	3.74	2.88	2.50	0.43	8.94	28.3	1.70	0.81	0.49	4.46	4.93	3.35
11	3.77	2.92	2.56	0.46	8.97	27.2	1.71	0.82	0.51	4.57	5.05	3.22
12	3.53	2.77	2.40	0.50	8.42	28.0	1.61	0.76	0.47	4.38	4.78	3.38
13	3.74	2.88	2.53	0.45	8.90	29.8	1.70	0.83	0.51	4.43	4.91	2.89
14	3.78	2.90	2.51	0.47	8.98	28.5	1.72	0.81	0.50	4.57	4.97	3.01
15	3.91	3.06	2.65	0.57	9.32	27.4	1.76	0.86	0.53	4.66	5.10	3.24
16	3.69	2.87	2.48	0.56	8.79	30.3	1.66	0.80	0.50	4.60	5.07	3.74
17	3.53	2.65	2.31	0.52	8.38	34.4	1.53	0.75	0.47	4.34	4.69	3.83
18	3.89	2.99	2.60	0.63	9.13	29.3	1.76	0.86	0.53	4.76	5.32	3.48
19	3.58	2.62	2.37	0.39	8.65	26.2	1.57	0.85	0.50	4.39	4.86	1.13
20	4.11	3.08	2.58	0.39	9.14	22.2	1.79	0.91	0.53	4.99	5.45	1.33
21	4.20	3.20	2.65	0.39	9.46	21.5	1.87	0.96	0.57	5.22	5.70	1.32
22	3.51	2.61	2.33	0.38	8.27	26.5	1.54	0.82	0.47	4.35	4.84	1.60
23	3.60	2.73	2.34	0.43	8.33	24.7	1.58	0.78	0.45	4.28	4.74	1.13

Table 16. Pooled within-locality variance-covariance matrix for males of *C. circumpicta*. Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4} to conserve space; thus "253"=0.0253.

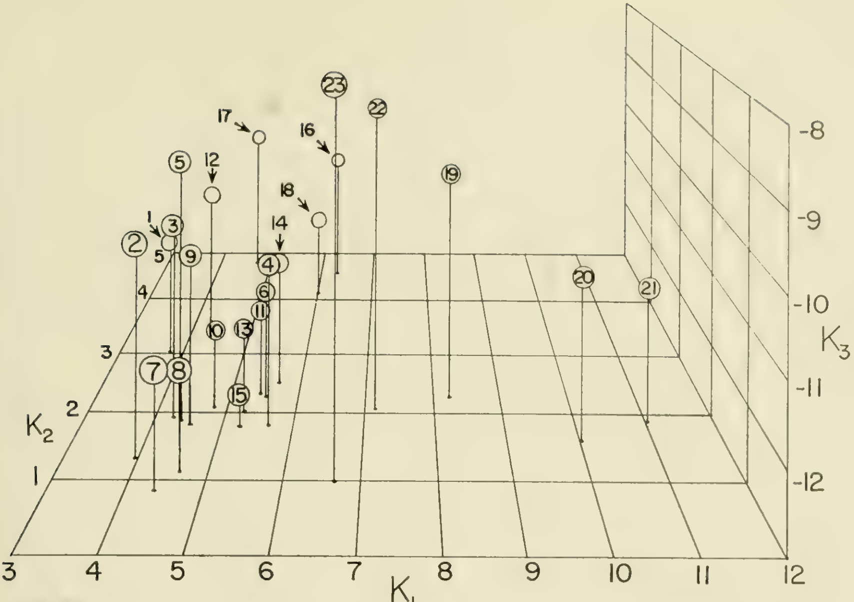
	Character											
Character	1	2	3	4	5	6	7	8	9	10	11	12
1	253	240	184	41	647	−1049	134	82	50	351	370	−38
2		394	304	62	1074	846	216	117	70	593	623	−86
3			284	64	908	983	176	97	60	504	528	−73
4				143	190	267	36	24	13	104	119	211
5					3503	2670	634	346	213	1864	1953	−259
6						141199	509	221	156	2148	2068	670
7							137	70	43	350	367	−33
8								49	25	191	198	2
9									19	120	125	−5
10										1256	1178	−69
11											1301	−49
12												4403

TABLE 17. Pooled within-locality variance-covariance matrix for females of *C. circumpicta.* Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4} to conserve space; thus "304"=0.0304.

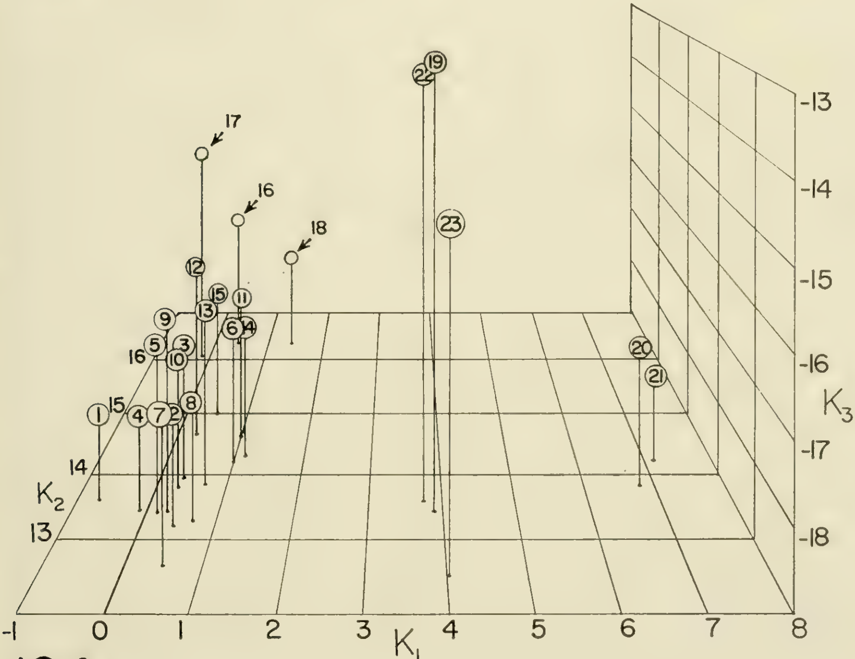
	Character											
Character	1	2	3	4	5	6	7	8	9	10	11	12
1	304	251	204	45	635	—2078	130	73	43	264	316	—106
2		258	187	40	567	—1950	117	66	39	244	285	—92
3			184	41	490	—1585	96	53	32	203	239	—95
4				63	98	—266	21	10	5	39	56	123
5					1767	—5664	308	179	104	663	815	—180
6						100873	—1039	—620	—343	—2390	—2543	97
7							72	37	22	133	157	—14
8								34	14	84	100	—23
9									12	47	56	—18
10										461	419	—68
11											607	17
12												3047

in males and 92.10% in females. The distributions of the means in the first three discriminant functions are shown in Figures 103 and 104. The localities fall into two loose clusters in both sexes, with localities 19-23 in one and all other localities in the other. The two clusters are not as widely separated in males as they are in females; however, there is still a distinct break between them because localities 19, 22, and 23 have high values in K_3, while the nearest localities in the other cluster have lower values. The results of the simultaneous testing procedure show that all combinations of pairs of means are significantly different at the 5% level except 6 vs. 11, 10 vs. 11, 19 vs. 22, and 22 vs. 23 for both sexes; 4 vs. 6, 11 vs. 14, 11 vs. 15, and 16 vs. 18 for males; and 2 vs. 3, 8 vs. 10, 11 vs. 13, 3 vs. 14, 6 vs. 14, 8 vs. 14, 10 vs. 14, 11 vs. 14, and 13 vs. 14 for females. Thus, several pairs within the clusters are not significantly different, but the nearest intercluster pairs are significantly different. Localities 16, 17, and 18 could be considered a subcluster; however, including samples from geographic areas between them and their nearest neighbors would probably destroy this appearance.

Sets of vectors (Figs. 105 and 106), plotted for the first two discriminant functions, show the geographic trends of the 12 characters when compared with Figures 103 and 104. Thus, specimens with high values in K_1 (the right-hand cluster) have high values for characters 1, 8, 10, and 11 and low values for characters 2, 3, 5, and 7; while specimens with low values in K_1 show the opposite trend (when all characters are considered simultaneously). Similarly, specimens high in K_2 are also high in characters 4 and 9, and low in 7 and 8.

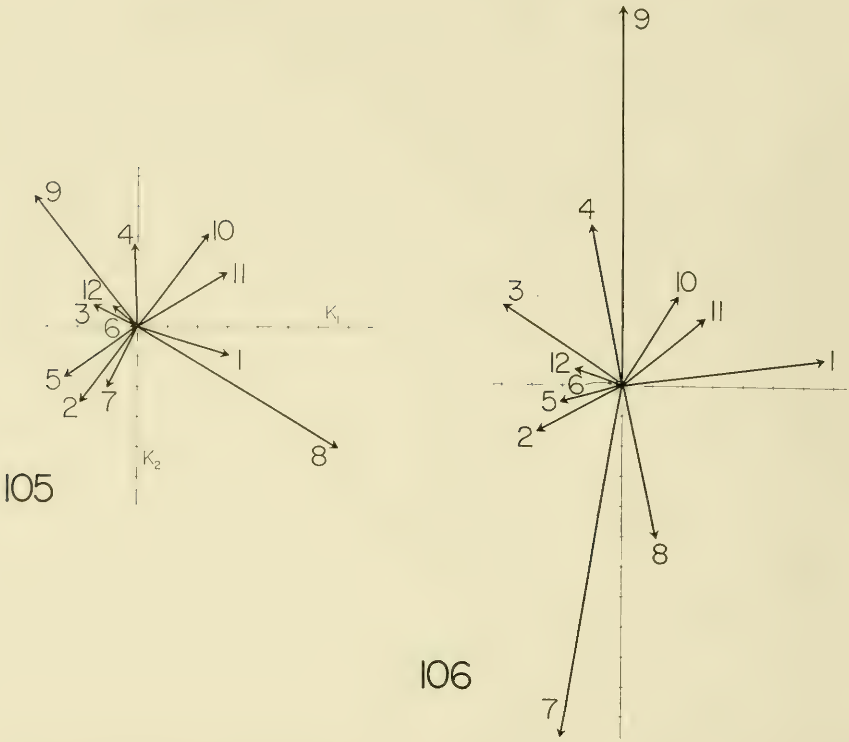


103



104

FIGS. 103-104. Distributions of the means of 23 localities for males (Fig. 103) and females (Fig. 104) of *C. circumpicta* in the first three discriminant functions (K_1, K_2, K_3), drawn as three-dimensional models, with numbered balls representing the means and vertical supports arising from the K_1, K_2 surface. Different sized balls indicate different distances from the viewer.



FIGS. 105-106. Vectors for the 12 characters of males (Fig. 105) and females (Fig. 106) of *C. circumpicta* for the first two discriminant functions. Each vector shows the change in the discriminant function that the corresponding character would produce if it varied independently. Units are same as in Figs. 103-104.

The results of the color analysis are shown in Figure 107. Populations from near the Gulf Coast and lower Rio Grande valley are nearly uniformly dark purplish to dark olive green, although in the vicinity of Corpus Christi, Texas, a small percentage of bright green, blue-green, and blue individuals occur. Most other populations contain individuals in bright reddish, green, and blue morphs in varying proportions. In general, reddish individuals are most common, followed by green and blue. In several scattered localities, reddish individuals compose nearly the entire population (southern New Mexico, southwestern and west-central Oklahoma, north-central Kansas, Nebraska, and North Dakota). In Missouri only blue to green individuals occur, while populations in southeastern Kansas and northeastern Oklahoma contain a higher percentage of these morphs than western populations. The southern-most sample in eastern Oklahoma contains an unusually high number of dark individuals. The North Dakota population is unique in containing about 15% black (or at least very dark purple) individuals. Thus, we

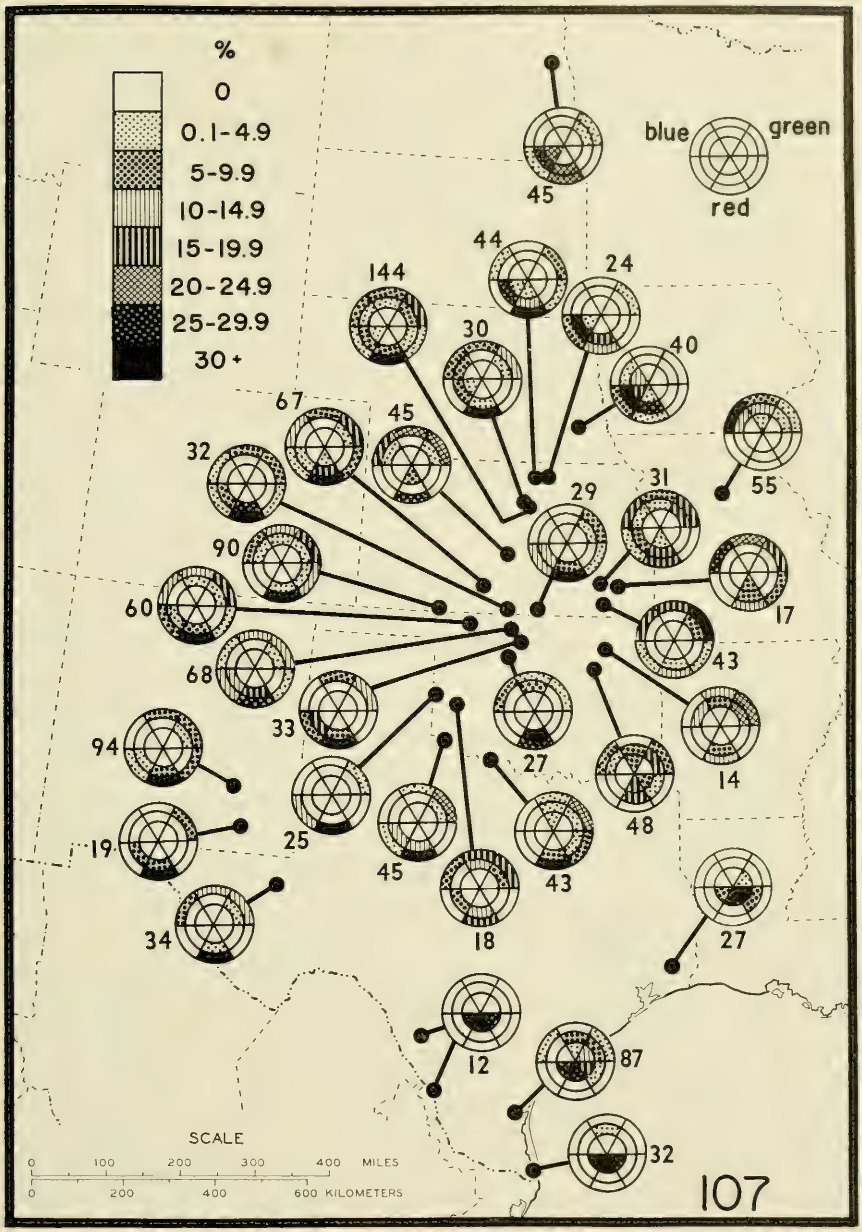

%
0
0.1-4.9
5-9.9
10-14.9
15-19.9
20-24.9
25-29.9
30+
blue
green
red
45
44
24
144
30
40
67
45
32
55
31
29
90
17
60
43
68
33
27
14
94
48
25
45
43
19
34
18
27
12
87
32
SCALE
0 100 200 300 400 MILES
0 200 400 600 KILOMETERS
107

FIG. 107. Results of color analysis of *C. circumpicta* using the color wheel. Different degrees of shading indicate different percentages of the sample (upper left). The positions of the three major colors are shown at upper right. Numbers show the sample size for each locality.

may divide the samples into two major groups: the rather uniform dark coastal populations and the quite heterogeneous, usually bright inland populations, which exhibit much intra- and interpopulation variation.

Considering the pattern of geographic variation shown by this species, I think it is best to recognize only two subspecies (Fig. 99): 1) *C. c. circumpicta*, characterized by narrow maculation, particularly a thin middle band, a relatively long labrum and wide head, and usually dark color, ranging from dark purplish to dark olive green, with occasional bright blue or green individuals; 2) *C. c. johnsoni*, having wider maculation, particularly a wider, often broadly rounded middle band; relatively short labrum and narrow head, and usually bright color, ranging from reddish to green to blue, with occasional brown or black individuals.

The recently described *C. c. salinae* was separated because of its small size, dull (not glossy) elytra, and brown or dark red color, with no blue or green individuals. The present analysis shows that populations of quite small individuals occur in several scattered localities. Although it was not measured, relatively dull elytra seem to be characteristic of populations from northern Kansas, Missouri, Nebraska, and North Dakota. The tendency for local populations to contain only one color morph seems not to be uncommon in this species. Thus, *C. c. salinae* does not seem sufficiently distinct to warrent its continued recognition.

C. circumpicta probably arose within its present range. Its closest relatives, *C. praetextata* and *C. californica*, occur in the southwestern United States and western Mexico. It is proposed that a common ancestor to the three became widespread from Texas to California during the late Tertiary. The rising mountains of the Cascadian Revolution and the drier, cooler climate of this time separated the ancestral species into at least three groups, which evolved into the modern species. Probably while this was occurring, proto-*circumpicta*, had already begun to become differentiated into coastal and inland forms, possibly in the form of a cline along the Rio Grande valley. Drier climates of the Pleistocene then extinguished intermediate populations in the upper Rio Grande valley. The fluctuating sea level of the Pleistocene probably "encouraged" *C. c. circumpicta* to disperse up many of the Texas rivers; today relict populations exist in the Dallas vicinity and the lower Rio Grande valley. *C. c. johnsoni* had not dispersed to Nebraska or central Missouri by mid-Pleistocene because the Nebraskan and Kansan glaciers covered these areas (or if it had reached these areas, it was driven back or exterminated). As it dispersed northeastward from its place of origin, *C. c. johnsoni* became more and more unlike the original stock, producing the entirely blue or green populations of Missouri and the entirely reddish populations near Lincoln, Nebraska. Central Missouri was apparently reached via southeastern Kansas.

The occurrence of reddish, green, and blue color morphs seems to have been a characteristic of the ancestral species of *C. circumpicta*, *C. praetextata*, and *C. californica*, because they occur in all three modern species. Thus, it is proposed that the coastal *C. c. circumpicta* has nearly lost this primitive character, while most populations of *C. c. johnsoni* have retained it. The bright green and blue morphs would seem to be at a great disadvantage in being camouflaged, and evidence presented earlier supports this (see section on ecological relationships of the adult). The pattern of color variation (Fig. 107) shows that, except for populations in northern Kansas, those populations with the highest percentage of bright reddish individuals occur in those regions that possess very red soil derived from the Permian redbeds (Fig. 108). This suggests that the bright green and blue morphs are gradually being lost in these areas. As populations from these areas dispersed northward into Kansas, Nebraska, and North Dakota, they encounted darker soils. The high frequency of darker red and purplish individuals from these localities indicates that evolution has occurred to produce better camouflaged individuals. The high percentage of rather bright blue and green individuals in southeastern Kansas and Missouri is difficult to explain; soils in these areas are generally dark. Perhaps dark green and dark purplish of *C. c. circumpicta* match very well the dark soils prevalent in the areas where it occurs.

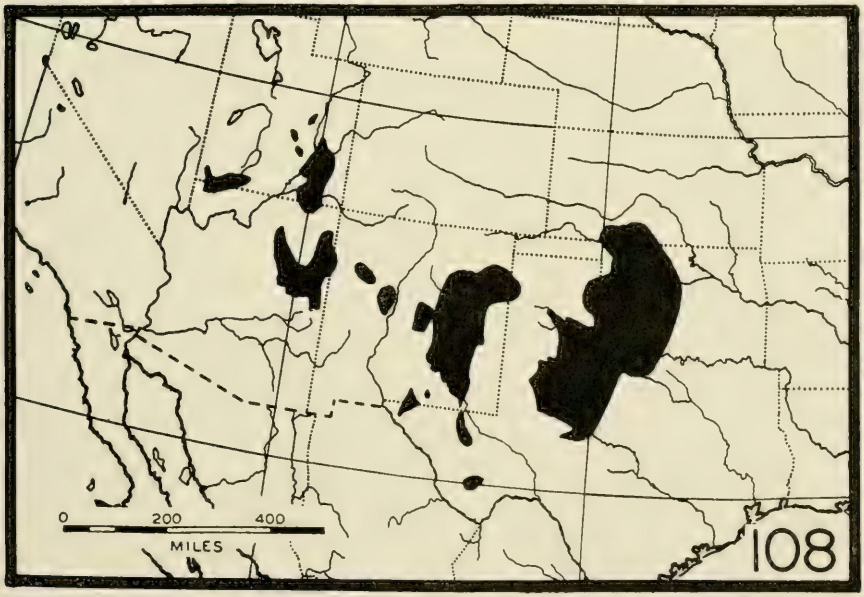


FIG. 108. Distribution of soils derived from the Permian redbeds. From map: Origin and distribution of United States soils, prepared by the Technical Development Service, Civil Aeronautics Administration and the Engineering Experimental Station, Purdue University (1946).

The wider markings of populations in southwestern Kansas, western Oklahoma, western Texas, and New Mexico seems to be an indirect result of the drier climate of these areas, which causes a white crust of salt to be present on saline habitats more of the time than in moister areas (see section on ecological relationships of the adult). The occurrence of widely maculate individuals in North Dakota seems to be a convergence that has taken place recently.

C. cuprascens

This species is most common between the Rocky and Appalachian Mountains (Fig. 109). The distribution by counties or states is the following:

GEORGIA; ALABAMA: Tuscaloosa; MISSISSIPPI: Warren; TENNESSEE: Shelby; KENTUCKY: Campbell, Fulton, Henderson, Kenton; OHIO; INDIANA: Posey, Putnam;

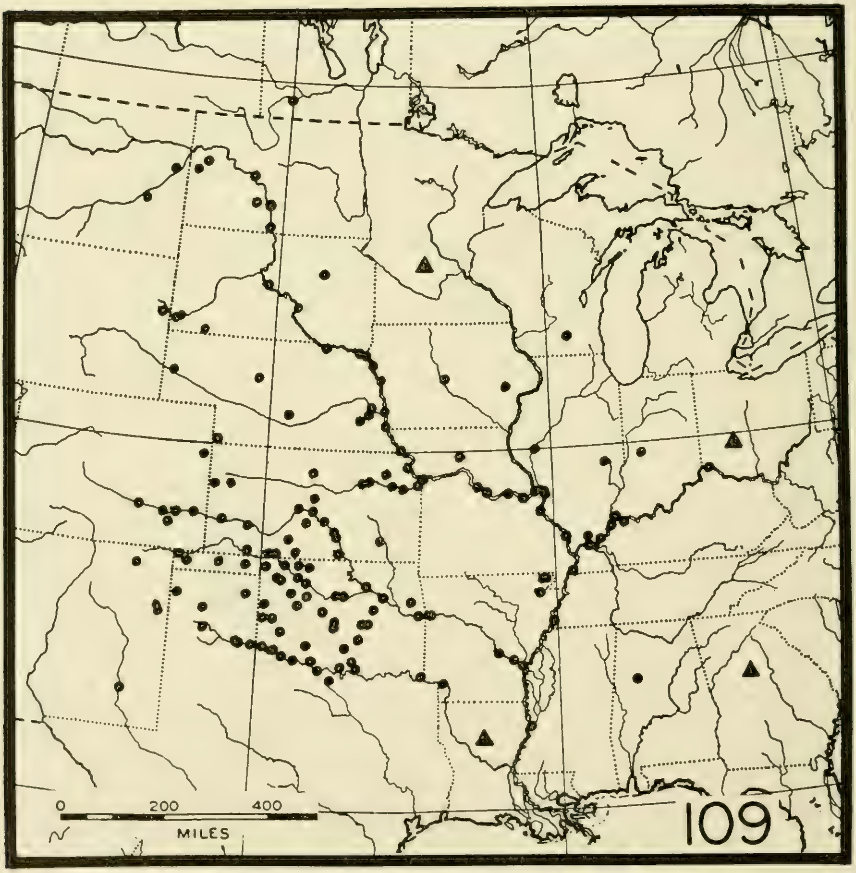


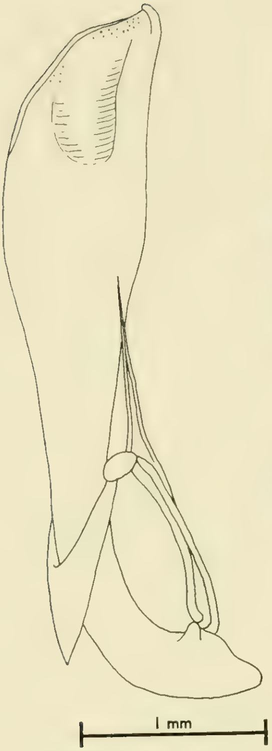
Fig. 109. Known distribution of *C. cuprascens*; triangle=state record.

ILLINOIS: Coles, Hardin, Jackson, Johnson, Masac, Morgan, Pope, Clair; WISCONSIN: Dane; MINNESOTA; IOWA: Johnson, Monona, Pottawatamie, Story, Woodbury; MISSOURI: Boone, Cooper, Franklin, Gasconade, Holt, Jefferson, Livingston, St. Charles, St. Louis; ARKANSAS: Arkansas, Clay, Craighead, Crawford, Desha, Jefferson, Lincoln, Miller, Sebastian; LOUISIANA; TEXAS: Childress, Cooke, Hall, Hardeman, Hartley, Hemphill, Hutchinson, Montague, Potter, Randall, Wichita, Wilbarger; OKLAHOMA: Alfalfa, Beaver, Beckham, Canadian, Cherokee, Cimarron, Cleveland, Comanche, Cotton, Custer, Dewey, Greer, Harper, Hughes, Jackson, Jefferson, Johnson, Kiowa, Logan, Love, Major, Marshall, McCurtain, Murray, Okfuskee, Payne, Pontotoc, Roger Mills, Sequoyah, Texas, Tillman, Tulsa, Woods, Woodward; KANSAS: Atchison, Barton, Clark, Clay, Douglas, Ellsworth, Finney, Ford, Gray, Hamilton, Johnson, Kearney, Kiowa, Leavenworth, Logan, McPherson, Meade, Pottawatomie, Reno, Rice, Riley, Sedgwick, Shawnee, Sumner, Wallace, Wyandotte; NEBRASKA: Buffalo, Cass, Dakota, Dixon, Douglas, Dundy, Knox, Otoe, Platte, Richardson, Scotts Bluff, Thomas; SOUTH DAKOTA: Brule, Clay, Fall River, Shannon, Spink, Union; NORTH DAKOTA: Billings, Burleigh, Emmons, Mc Kenzie, Mc Lean, Mercer, Morton; MANITOBA; MONTANA: Custer, Dawson; WYOMING: Niobrara; COLORADO: Bent, Denver, Otero, Prowers, Pueblo, Yuma; NEW MEXICO: Chaves, Colfax, Quay. Towns that could not be located: Eastport and Eastbrook, Iowa; Wicks, Missouri. Doubtful records: Moscow, Latah Co., Idaho; Logan Canyon, Cache Co.?, Utah.

A closely related form, which has been considered a subspecies of *C. cuprascens* (Horn, 1930; Leng, 1902), a subspecies of *C. macra* (Vaurie, 1951), or a separate species (G. Horn, 1876; Schaupp, 1883-1884), is *puritana* G. Horn. It is found along the Connecticut River in New Hampshire (Sullivan Co.), Massachusetts (Hampden and Hampshire Cos.), and Connecticut (Hartford Co.), and around Chesapeake Bay in Maryland (Calvert and St. Marys Cos.). State records exist for New York and Virginia. Some specimens appear to be labelled "Windsor, Can.," which is in southern Ontario. Wallis (1961) does not mention this record from Canada, and the labels probably should read "Windsor, Connecticut," where this form has been collected. After examining the adult morphology, including the male genitalia, I think *puritana* should be considered a separate species, one that is more closely related to *C. cuprascens* than to *C. macra*. The three species are compared in Table 18. In certain characters, *C. puritana* is somewhat intermediate between *C. cuprascens* and *C. macra*. Because of its distinct com-

TABLE 18. Comparison of seven characters in *C. cuprascens*, *C. puritana*, and *C. macra*.

Character	*C. cuprascens*	*C. puritana*	*C. macra*
Shape of posterio-lateral emargination of ♀ elytra	Acute	Acute	Rectangular
Shape of ♀ elytral apices	Rounded	Acute or occas. truncate	Acute
Depth of elytral punctation	Deep	Deep to shallow	Shallow
Elytral surface	Shiny	Shiny, occas. dull	Dull
Typical shape of apex of middle band	Globose or not enlarged	Globose or not enlarged	Recurved or triangular
Shape of aedeagus	More slender (Fig. 93)	Thicker (Fig. 110)	Thicker (Fig. 112)
Shape of tooth of inner sac	Long and acute (Fig. 95)	Long and acute (Fig. 111)	Shorter and blunt (Fig. 113)



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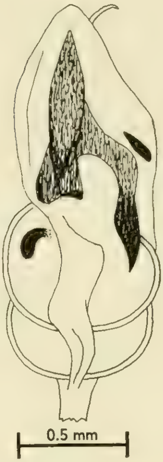

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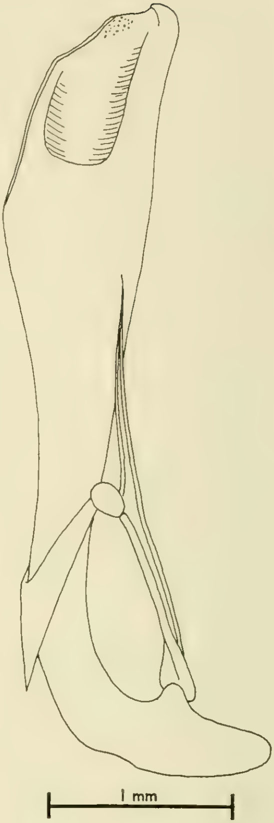

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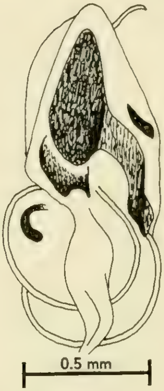

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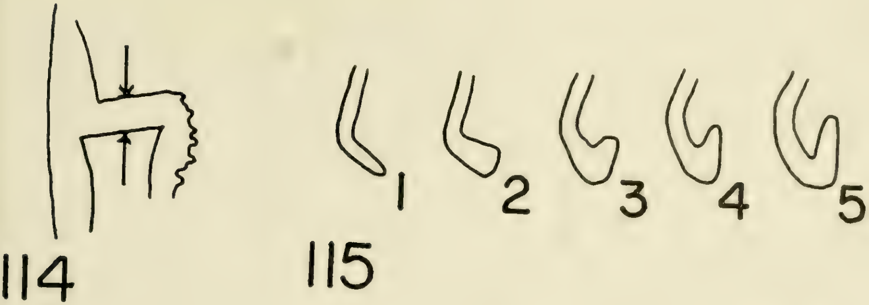
FIG. 110. Aedeagus of *C. puritana* (Windsor, Connecticut), dorsal aspect. FIG. 111. Inner sac of aedeagus of *C. puritana*, ventral aspect. FIG. 112. Aedeagus of *C. macra* (Ness County, Kansas), dorsal aspect. FIG. 113. Inner sac of aedeagus of *C. macra*, ventral aspect.

bination of characters, and because it is geographically isolated from *C. cuprascens* and *C. macra*, I have separated it taxonomically. As a test, it was included in the statistical analysis along with *C. cuprascens.*

In recent years, no subspecies have been recognized. The following forms have been described within the species *C. cuprascens*:

Cicindela cuprascens Leconte, 1852. Type locality: Arkansas River (types bear green paper circles, signifying "Kansas, Nebraska, and westward")
Cicindela cuprascens amnicola Casey, 1913. Type locality: Kentucky, Illinois, and Missouri.
Cicindela mundula Casey, 1913. Type locality: Vicksburg, Mississippi.

In the study of geographic variation, the following characters were measured : (1) length of left elytron; (2) width of left elytron; (3) width of



Figs. 114-115. Illustrations of certain characters measured on elytra of *C. cuprascens*, *C. puritana*, and *C. macra*; Fig. 114, width of middle band; Fig. 115, arbitrary units for shape of apex of middle band.

labrum; (4) length of labrum, including tooth; (5) width of middle band at a specified place (Fig. 114); (6) width of head; (7) shape of apex of middle band in arbitrary units (Fig. 115); (8) color of elytra, using color wheel.

Specimens from nine localities were measured; the localities and sample sizes are given in Table 19. Sample sizes were adequate from all the localities; however, specimens from several localities in Alabama and Missouri were lumped.

Table 19. Localities and sample sizes of the specimens of *Cu puritana* and *C. cuprascens* measured.

Locality	N	
	♂	♀
C. puritana:		
1. CONNECTICUT, Hartford Co., Windsor	12	12
C cuprascens:		
2. ALABAMA, Tuscaloosa Co., several localities	12	7
3. MISSOURI, St. Louis Co., St. Louis; St. Charles Co., St. Charles	12	12
4. IOWA, Pottawattamie Co., Council Bluffs	12	12
5. KANSAS, Douglas Co.	12	12
6. KANSAS, Clark Co., 8 mi. s. of Sitka	12	12
7. OKLAHOMA, Alfalfa Co., 3 mi. n., 5 e. of Cherokee	12	12
8. OKLAHOMA, Cleveland Co.	12	12
9. COLORADO, Bent Co., Las Animas	12	12

The means for the characters and localities are given in Tables 20 and 21. Analyses of variance of the individual characters showed that there are significant differences ($p < 0.01$) among the means of all characters for both sexes except character 2 for females, which is significant at the 5% level. Pooled within-locality variance-covariance matrices are given in Tables 22 and 23. The sums of the among-locality variance components are 82.768 for

TABLE 20. Means of nine localities (see Table 19) and seven characters for males of *C. puritana* and *C. cuprascens*. Values for characters 1-6 are in mm.

				Character			
Locality	1	2	3	4	5	6	7
1	7.32	2.01	1.39	0.64	0.31	2.84	1.54
2	6.73	1.89	1.34	0.59	0.27	2.62	2.67
3	7.16	1.90	1.41	0.63	0.30	2.90	2.06
4	7.46	2.00	1.47	0.63	0.36	2.91	2.43
5	7.38	1.92	1.44	0.63	0.34	2.91	2.22
6	7.79	2.04	1.56	0.70	0.46	3.15	2.50
7	7.46	2.02	1.53	0.68	0.43	3.08	2.21
8	7.46	2.02	1.51	0.66	0.43	3.05	2.54
9	7.57	2.03	1.54	0.66	0.45	3.00	2.96

TABLE 21. Means of nine localities (see Table 19) and seven characters for females of *C. puritana* and *C. cuprascens*. Values for characters 1-6 are in mm.

				Character			
Locality	1	2	3	4	5	6	7
1	7.67	2.18	1.43	0.64	0.34	3.03	1.60
2	7.26	2.06	1.40	0.57	0.28	2.84	2.10
3	7.96	2.13	1.57	0.66	0.32	3.19	2.53
4	7.99	2.18	1.59	0.65	0.38	3.23	2.20
5	7.97	2.14	1.59	0.67	0.37	3.22	2.43
6	8.09	2.17	1.60	0.68	0.46	3.34	2.32
7	7.91	2.17	1.61	0.69	0.43	3.29	2.32
8	7.96	2.18	1.61	0.66	0.41	3.24	2.26
9	8.04	2.16	1.60	0.67	0.43	3.23	2.63

TABLE 22. Pooled within-locality variance-covariance matrix for males of *C. puritana* and *C. cuprascens*. Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "940"=0.0940.

					Character			
		1	2	3	4	5	6	7
Character	1	940	222	182	85	16	267	383
	2		79	51	25	5	83	74
	3			50	21	—1	64	70
	4				20	—5	29	21
	5					67	—0	—30
	6						128	117
	7							4332

Table 23. Pooled within-locality variance-covariance matrix for females of *C. puritana* and *C. cuprascens*. Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "751"=0.0751.

		Character						
		1	2	3	4	5	6	7
Character	1	751	137	108	71	39	254	−161
	2		48	27	16	8	53	−28
	3			37	14	8	45	−54
	4				16	2	28	−5
	5					56	7	9
	6						129	−128
	7							3595

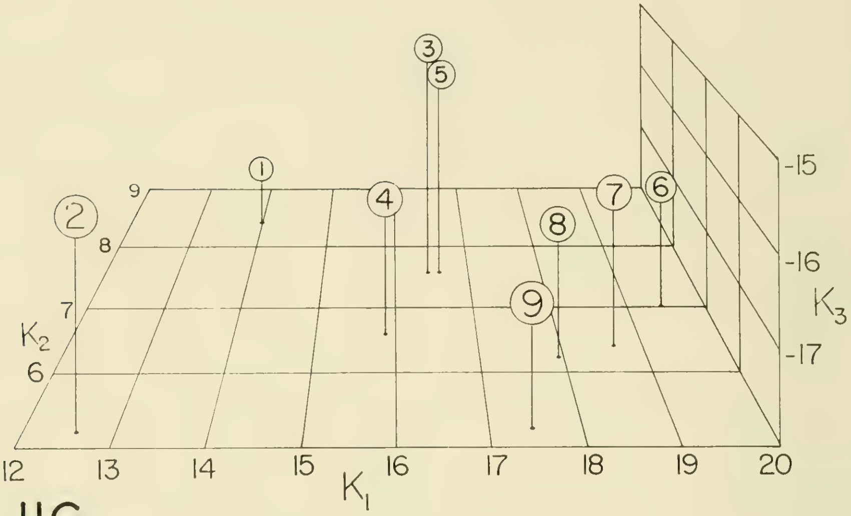
males and 55.300 for females. The first three components for males and the first two for females are highly significant ($p < 0.01$), and the fourth component for males is significant at the 5% level. The third component for females is on the borderline of being significant at the 5% level. The first three functions account for 83.47% of the variance (among localities relative to that within) in males and 93.13% in females. The distributions of the means in the first three discriminant functions are shown in Figures 116 and 117. Localities 1 and 2 are rather distantly separated from the others, which form a loose cluster in males and a tighter one in females.

The results of the simultaneous testing procedure show that all combinations of pairs of means are significantly different at the 5% level except 3 vs. 5 for both sexes, and 3 vs. 4, 4 vs. 5, 4 vs. 8, 4 vs. 9, 5 vs. 8, 5 vs. 9, 6 vs. 7, and 8 vs. 9 for females. Thus, the samples of *C. puritana* and *C. cuprascens* from Alabama are quite different from each other and from the other samples, which are more similar to each other.

Sets of vectors (Figs. 118 and 119), plotted for the first two functions, show the geographic trends of the seven characters when compared with Figures 116 and 117. Specimens from localities 1 and 2 are characterized by having relatively wider elytra and narrower heads. Specimens from western Kansas, Oklahoma, and Colorado (localities 6-9) have wider labra and middle bands and narrower elytra.

The results of the color analysis are shown in Figure 120. Populations northeast of eastern Kansas (including *C. puritana*) consist mostly of dark red-green, green, or blue-green individuals, with occasional blue individuals. Southwest of eastern Kansas, many individuals are reddish, often bright red.

On the basis of the statistical analysis, the specimens from Alabama seem distinct enough to separate as a subspecies; however, this is probably not wise at present because no samples were measured from areas between there and



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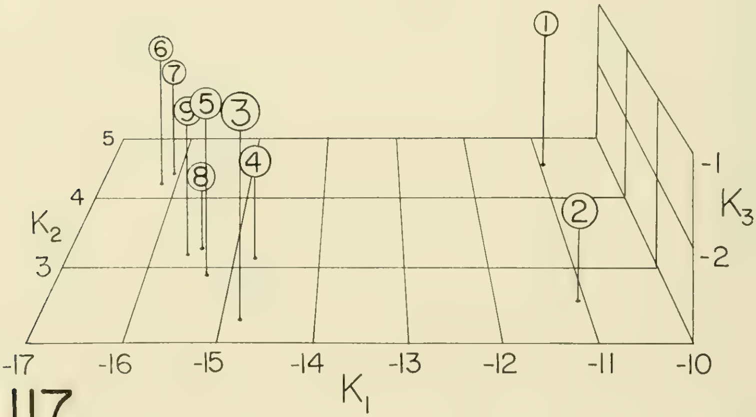

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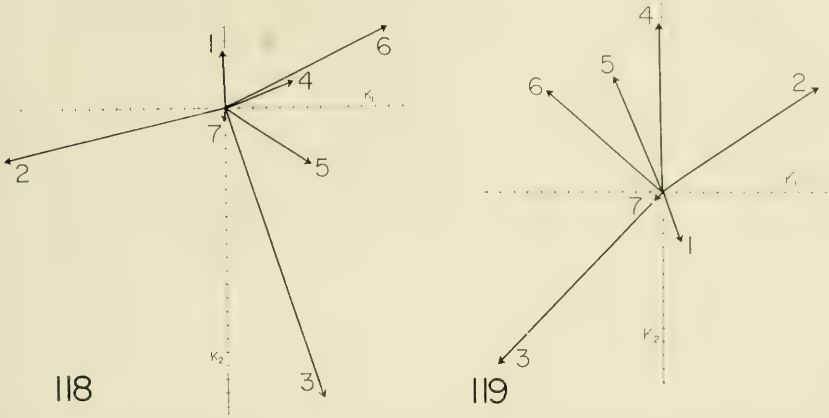
FIGS. 116-117. Distributions of the means of the nine localities for males (Fig. 116) and females (Fig. 117) of *C. puritana* and *C. cuprascens* in the first three discriminant functions (K_1, K_2, K_3), drawn as three-dimensional models, with numbered balls representing the means and vertical supports arising from the K_1, K_2 surface. Different sized balls indicate different distances from the viewer. The models are viewed from opposite directions, relative to the clusters.


1
6
4
K_1
7
2
5
K_2
3
118
4
5
6
2
K_1
7
1
K_2
3
119

Figs. 118-119. Vectors for the seven characters of males (Fig. 118) and females (Fig. 119) of *C. puritana* and *C. cuprascens* for the first two discriminant functions. Each vector shows the change in the discriminant function that the corresponding character would produce if it varied independently. Units are same as in Figs. 116-117.

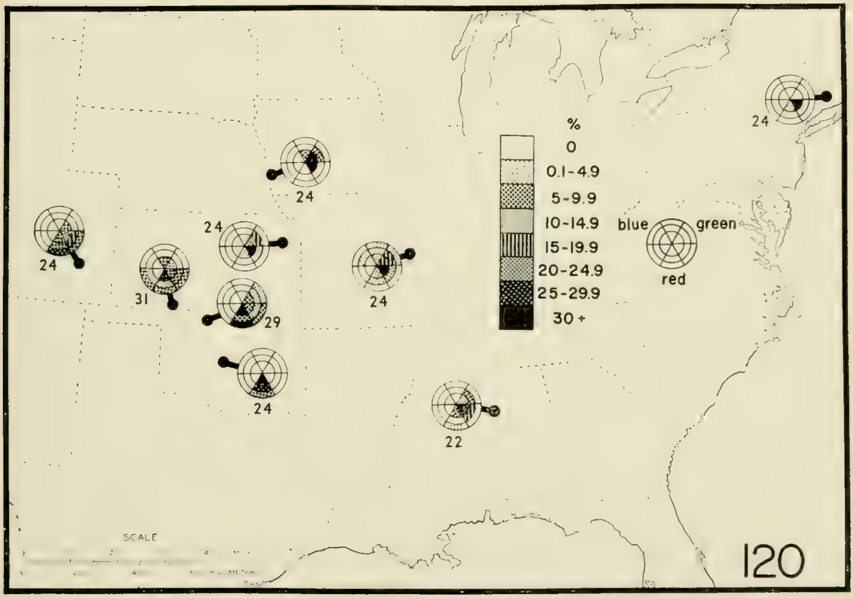

24
24
%
0
0.1-4.9
5-9.9
10-14.9
15-19.9
20-24.9
25-29.9
30+
24
blue
green
red
31
24
29
24
24
22
SCALE
120

Fig. 120. Results of color analysis of *C. puritana* and *C. cuprascens* using the color wheel. Different degrees of shading indicate different percentages of the sample. The position of the three major colors are shown at right center. Numbers show the sample size for each locality.

Oklahoma or Missouri. The few specimens I have examined from these intervening areas, however, appear more like those from Missouri or Oklahoma than from Alabama. I have not seen specimens from Georgia. The color analysis suggests the populations in southern Kansas, Colorado, and Oklahoma, with many red individuals, might be worth naming, but the statistical analysis shows that the females are not distinct enough, although males are quite distinct. Thus, I recognize no subspecies within *C. cuprascens*. As the statistical analysis showed, *C. puritana* is quite different from *C. cuprascens*, even though only one of the characters in Table 18 was measured.

The closest relatives to *C. cuprascens* are *C. puritana* and *C. macra*. The former is restricted to the northern Atlantic Coastal Plain, while the latter is sympatric with *C. cuprascens* throughout most of their ranges. However, *C. macra* does not occur east of the Mississippi River in the South, as *C. cuprascens* does. This could indicate that *C. cuprascens* and *C. macra* evolved on opposite sides of the Mississippi valley, but not necessarily so. No other explanation is readily apparent. It does appear, at least, that *C. cuprascens* was once more widespread along the southeastern coastal plain than it now is, since the Alabama populations are so far separated from other known populations. As its coastal plain populations were exterminated by climatic changes during the Pleistocene, the more northeastern ones apparently became isolated and evolved into *C. puritana*. The spread of *C. cuprascens* northwestward into the range of *C. macra* has probably occurred rather recently (late Pleistocene), since populations in this area are rather similar. Its spread into the Pecos River system probably occurred via the Canadian River through northwestern Texas (the headwaters of the two river systems are very close in New Mexico).

As is the case in other species, the predominance of red color in populations from southern Kansas, Oklahoma, and Colorado is almost certainly due to their living on red soils (or having recently dispersed from areas of red soil). Red individuals also occur in New Mexico, Texas, Arkansas, Wyoming, and Montana.

C. fulgida

This is primarily a northern species, which is most common in the Great Plains north of Texas (Fig. 121). Its distribution by counties or states is as follows:

MANITOBA; SASKATCHEWAN; ALBERTA; MONTANA: Gallatin, Prairie, Roosevelt, Sheridan; NORTH DAKOTA: Benson, Bottineau, Burke, Burleigh, Dickey, Divide, Dunn, Grand Forks, McLean, McHenry, Mercer, Montrail, Oliver, Pierce, Roulette, Slope, Stutsman; MINNESOTA; SOUTH DAKOTA: Beadle, Brookings, Edmund, Fall River, Kingsbury; WYOMING: Albany, Carbon, Goshen, Weston; COLORADO: Arapahoe, Bent, Conejos, Crowley, El Paso, Fremont, Huerfano, Larimer, Logan, Otero, Prowers, Sedgwick, Summit,

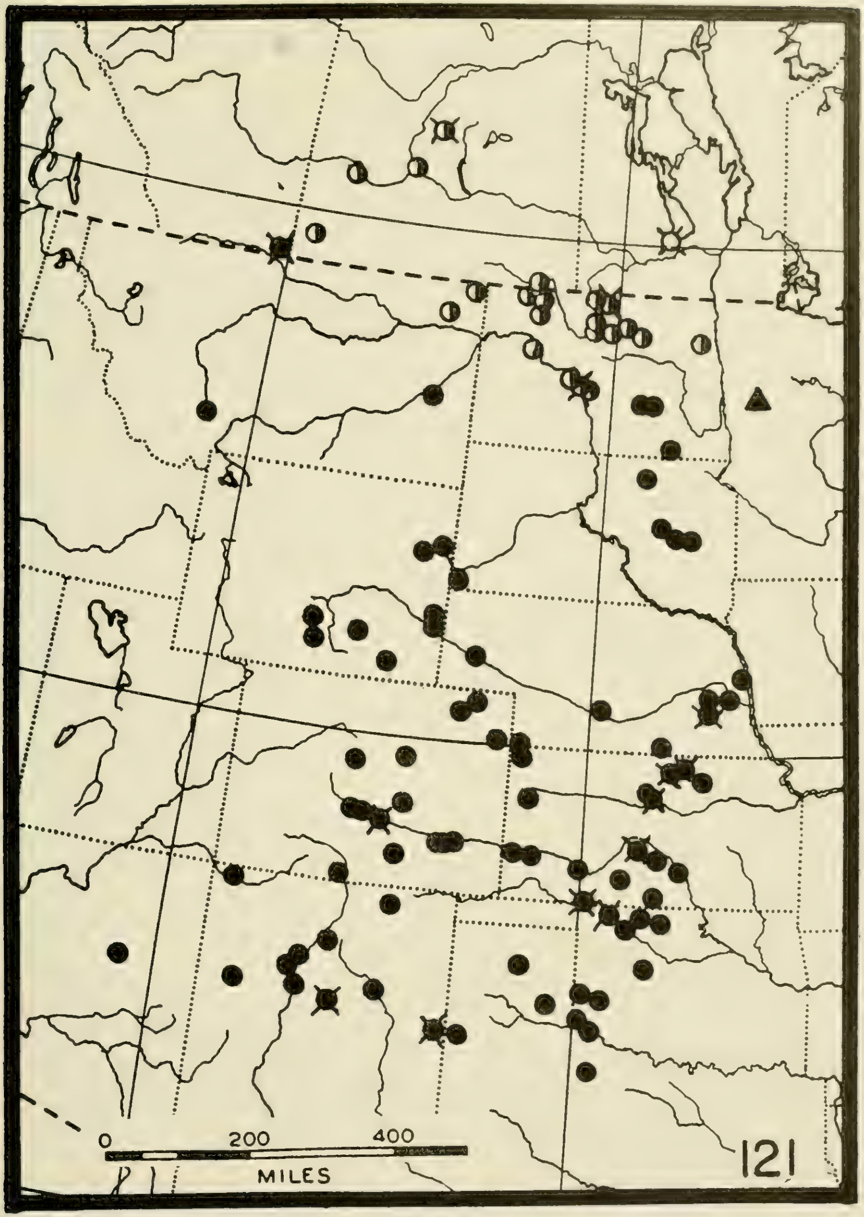


Fig. 121. Known distribution of *C. fulgida.* Open circle=*C. f. westbournei,* shaded circle=*C. f. fulgida,* half-shaded circle=intergrade population, triangle=state record, circles with "X" are localities included in the statistical analysis.

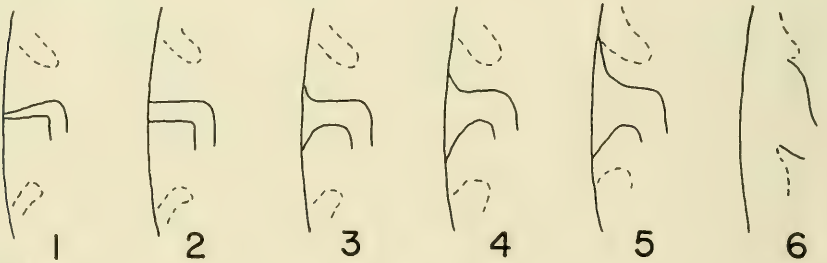
Weld, Yuma; NEBRASKA: Dawson, Douglas, Dundy, Lancaster, Morrill, Nuckolls, Saunders; KANSAS: Barber, Cheyenne, Clark, Clay, Cloud, Ford, Hamilton, Kearney, Kiowa, Lincoln, Reno, Republic, Sedgwick, Stafford, Wallace; OKLAHOMA: Alfalfa, Beckham, Blaine, Harmon, Jackson, Woods; TEXAS: Bailey, Donley, Hemphill, Hutchinson, Knox; NEW MEXICO; Bernalillo, Colfax, Guadalupe, Sandoval, San Juan, Torrance, Valencia; ARIZONA: Navajo. *Doubtful localities:* "Fla." and Woodward (La Salle Co.?), Texas.

The following forms have been described within this species:

Cicindela fulgida Say, 1823. Type locality: Missouri Territory, near the mountains on the Platte and Arkansas Rivers.
Cicindela fulgida elegans Calder, 1922. Type locality: Westbourne, Manitoba, Canada. *Preoccupied.*
Cicindela fulgida subnitens Calder, 1922. Type locality: Lincoln, Nebraska.
Cicindela fulgida westbournei Calder, 1922. New name for *C. f. elegans.*
Cicindela fulgida pseudowillistoni W. Horn, 1938. Type locality: Lake Como, southern Wyoming.

In recent years, two subspecies have been recognized: *C. f. westbournei*, the small, dark colored northern form, and *C. f. fulgida*, the bright, usually red southern form.

In studying geographic variation, the following characters were measured: (1) length of left elytron; (2) width of left elytron; (3) width of labrum; (4) length of labrum, including tooth; (5) shape of base of middle band in arbitrary units (Fig. 122); (6) smallest width of transverse portion of middle band (Fig. 123). Specimens from 14 localities were measured; the localities and sample sizes are given in Table 24. Sample sizes were adequate except for two localities each in Canada and New Mexico. Specimens from two localities in Saskatchewan and two in Colorado were lumped into one sample each.



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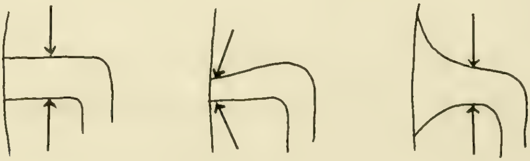

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FIGS. 122-123. Illustrations of certain characters measured on elytra of *C. fulgida*; FIG. 122, arbitrary units for shapes of base of middle band; FIG. 123, smallest width of transverse portion of middle band.

Table 24. Localities and sample sizes of the specimens of *C. fulgida* measured.

Locality	N ♂	N ♀
1. MANITOBA, Westbourne	12	12
2. SASKATCHEWAN, Route 14, s.e. of Blucher; between Clavet and Elston	6	2
3. ALBERTA, Onefour	5	6
4. NORTH DAKOTA, Bottineau Co., near Bottineau	12	12
5. NORTH DAKOTA, Oliver Co., Sect. 35, Twp. 144, Rg. 83	12	12
6. COLORADO, Fremont Co., 3 mi. s. of Penrose, near Portland	9	12
7. NEBRASKA, Lancaster Co., Lincoln (west edge)	12	11
8. KANSAS, Republic Co., ½ mi. e., 1 s. of Talmo	10	12
9. KANSAS, Republic Co., 4 mi. w., 1 s. of Kackley	12	12
10. KANSAS, Lincoln Co., 3 mi. w., 2 s. of Barnard	12	12
11. KANSAS, Stafford Co., 11 mi. n.e. of Hudson	12	12
12. KANSAS, Clark Co., Englewood	12	12
13. OKLAHOMA, Woods Co., 2.5 mi. s.w. of Plainview	11	8
14. NEW MEXICO, Roosevelt Co., 4 mi. e., 1 s. of Arch	4	3
15. NEW MEXICO, Torrance Co., 4 mi. s.e. of Willard	2	8

The means for the characters and localities are given in Tables 25 and 26. Analyses of variance of the individual characters showed that there are significant differences ($p < 0.01$) among the means of all characters for both sexes. Pooled within-locality variance-covariance matrices are given in Tables 27 and 28. The sums of the among-locality variance components are 83.504 for males and 69.975 for females. The first two components for males and the first three for females are highly significant ($p < 0.01$), and the third component for males is significant at the 5% level. The first three functions account for 96.50% of the variance (among localities relative to that within) in males and 94.63% in females. The distributions of the means in the first three discriminant functions are shown in Figures 124 and 125. Localities in the central United States and eastern New Mexico form a tight cluster, while the other localities are rather widely separated from one another and from the cluster.

The results of the simultaneous testing procedure show that all combinations of pairs of means are significantly different at the 5% level except 7 vs. 10, 9 vs. 11, 9 vs. 13, 11 vs. 12, 11 vs. 13, 12 vs. 13, 8 vs. 14, and 11 vs. 14 for both sexes; 8 vs. 10, 9 vs. 10, 9 vs. 12, 10 vs. 11, 10 vs. 12, 10 vs. 13, 9 vs. 14, and 10 vs. 14 for males; and 7 vs. 13, 8 vs. 9, 12 vs. 14, and 13 vs. 14 for females. Thus, the members of the cluster are generally not significantly different from one another, while the isolated samples are different from one another and the cluster.

Sets of vectors (Figs. 126 and 127), plotted for the first two functions, show geographic trends in the six characters when compared with Figures

TABLE 25. Means of 15 localities (see Table 24) and six characters for males of *C. fulgida*. Values for characters 1-4 and 6 are in mm.

Locality	Character 1	2	3	4	5	6
1	6.56	2.01	1.62	0.78	4.46	0.90
2	6.64	2.07	1.62	0.74	4.05	1.05
3	7.38	2.19	1.81	0.87	4.88	1.06
4	6.91	2.09	1.72	0.83	3.87	0.85
5	6.66	2.02	1.63	0.76	3.34	0.78
6	7.30	2.20	1.81	0.90	4.11	0.92
7	6.83	2.06	1.63	0.77	2.60	0.70
8	7.05	2.11	1.69	0.81	2.62	0.83
9	7.04	2.07	1.68	0.80	2.37	0.71
10	6.92	2.07	1.67	0.78	2.39	0.73
11	6.98	2.08	1.70	0.80	2.37	0.72
12	6.92	2.07	1.68	0.77	2.12	0.63
13	7.01	2.11	1.69	0.80	2.10	0.67
14	7.26	2.16	1.77	0.83	2.75	0.83
15	6.73	2.10	1.65	0.80	5.60	1.34

TABLE 26. Means of 15 localities (see Table 24) and six characters for females of *C. fulgida*. Values for characters 1-4 and 6 are in mm.

Locality	Character 1	2	3	4	5	6
1	6.94	2.21	1.72	0.86	3.84	0.81
2	7.04	2.25	1.73	0.84	3.40	0.88
3	7.40	2.39	1.87	0.94	4.28	1.02
4	7.22	2.32	1.84	0.93	3.48	0.82
5	6.95	2.17	1.73	0.85	2.97	0.74
6	7.69	2.42	1.95	1.00	3.26	0.93
7	7.04	2.19	1.71	0.83	2.27	0.61
8	7.20	2.18	1.76	0.87	2.20	0.76
9	7.26	2.21	1.76	0.88	2.13	0.71
10	6.98	2.13	1.70	0.81	2.18	0.67
11	7.26	2.24	1.79	0.86	2.17	0.70
12	7.26	2.25	1.78	0.84	2.02	0.66
13	7.25	2.26	1.76	0.87	2.08	0.64
14	7.39	2.29	1.84	0.89	2.10	0.81
15	7.00	2.18	1.73	0.86	5.03	1.30

124 and 125. Specimens with high values in K_1 have longer labra, wider markings, and relatively shorter elytra. Specimens with high values in K_2 have wide labra, narrow elytra (in males; wide in females), and narrower middle bands.

The results of this analysis show that, except for locality 15, there are no

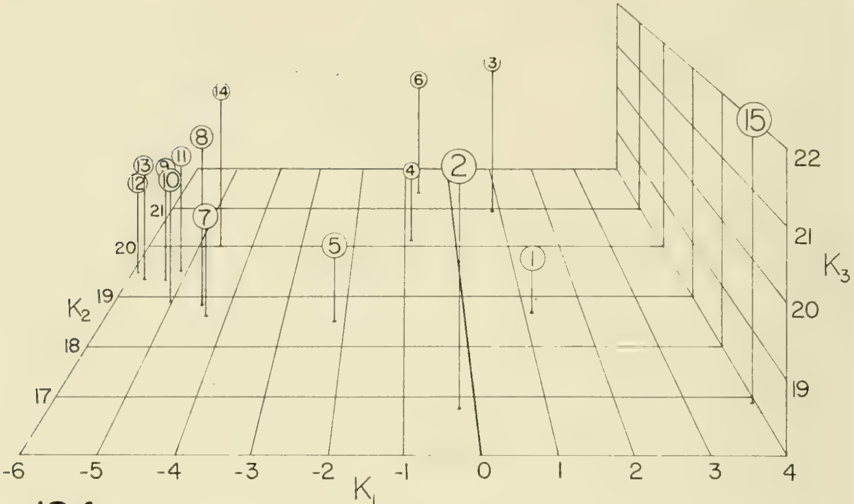
Table 27. Pooled within-locality variance-covariance matrix for males of *C. fulgida.* Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "690"=0.0690.

Character	1	2	3	4	5	6
1	690	140	137	90	274	129
2		49	36	23	67	29
3			42	24	64	30
4				23	33	18
5					1549	228
6						119

Table 28. Pooled within-locality variance-covariance matrix for females of *C. fulgida.* Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "691"=0.0691.

Character	1	2	3	4	5	6
1	691	160	141	103	114	77
2		62	38	27	16	19
3			42	27	23	15
4				26	5	11
5					2326	231
6						153

clear groupings that could be called subspecies. The tight cluster that is separated from other samples is probably an artifact caused by the nonrandom geographical distribution of the samples; if samples had been included from South Dakota, Wyoming, and Montana, they would probably fill in the gap. There appears to be a gradual cline running from larger, narrowly marked populations in the south to smaller, widely marked northern populations. Thus, on the basis of this analysis alone, the subspecies *C. f. westbournei*, representing one end of a cline, cannot be recognized. However, a character that was not measured sets it apart from all other populations: the shape of the apex of the aedeagus. In specimens from Westbourne, Manitoba, the apex of the aedeagus is rather evenly tapered and comparatively blunt; in specimens from all other localities, it is more prolonged and slender (Figs. 128-136). Another characteristic of specimens from Westbourne is their dark dorsal color, ranging from dark purplish red to black, often with a bluish sheen. Only three out of 39 specimens before me, or about 7.5%, have brighter colors (two are reddish, one is yellow-green). Specimens from other Canadian localities, northeastern Montana, and northern North Dakota exhibit a great variety of colors, ranging from dark purple to red to red-green to green to blue-green to blue to purple-blue. Green-red specimens are also



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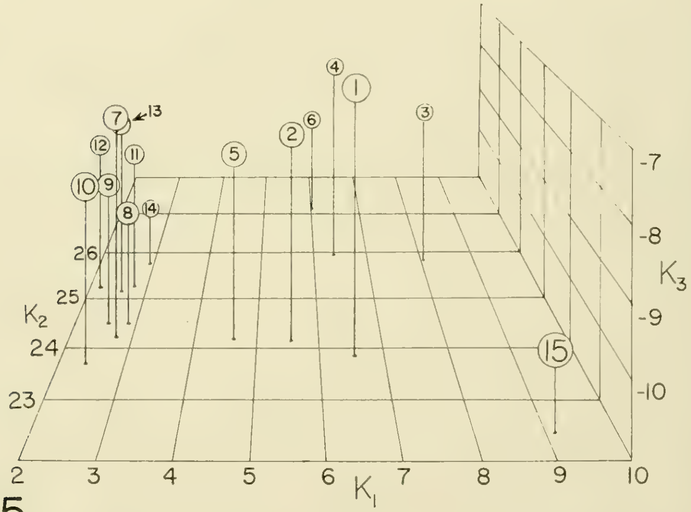

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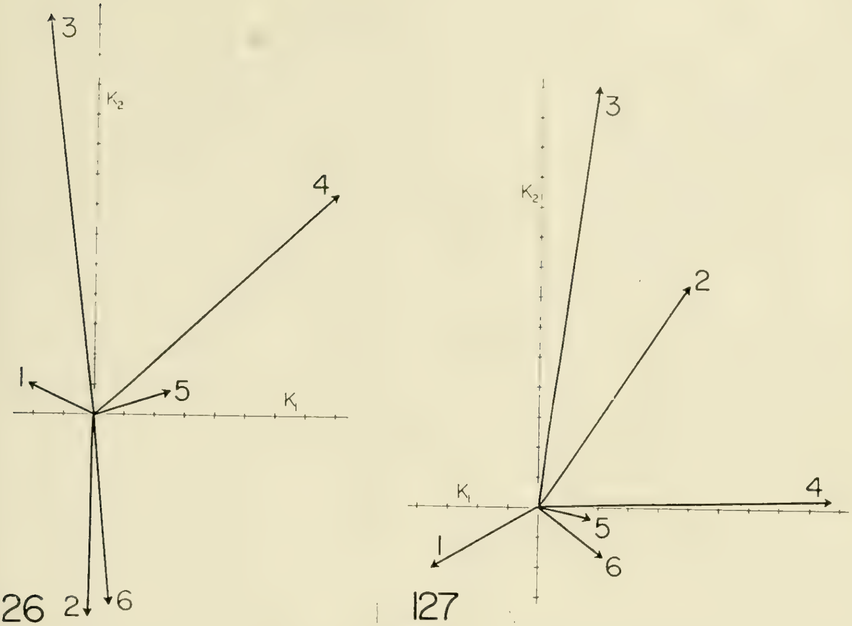
FIGS. 124-125. Distributions of the means of the 15 localities for males (Fig. 124) and females (Fig. 125) of *C. fulgida* in the first three discriminant functions (K_1, K_2, K_3), drawn as three-dimensional models, with numbered balls representing the means and vertical supports arising from the K_1, K_2 surface. Different sized balls indicate different distances from the viewer.

known from southwestern Montana, southern Wyoming, and central Colorado. The population at Grants, New Mexico, is said to contain many blue individuals (Rumpp, *in litt.*). The population at Lincoln, Nebraska, contains about 40% dark purple or black individuals. Specimens examined from other



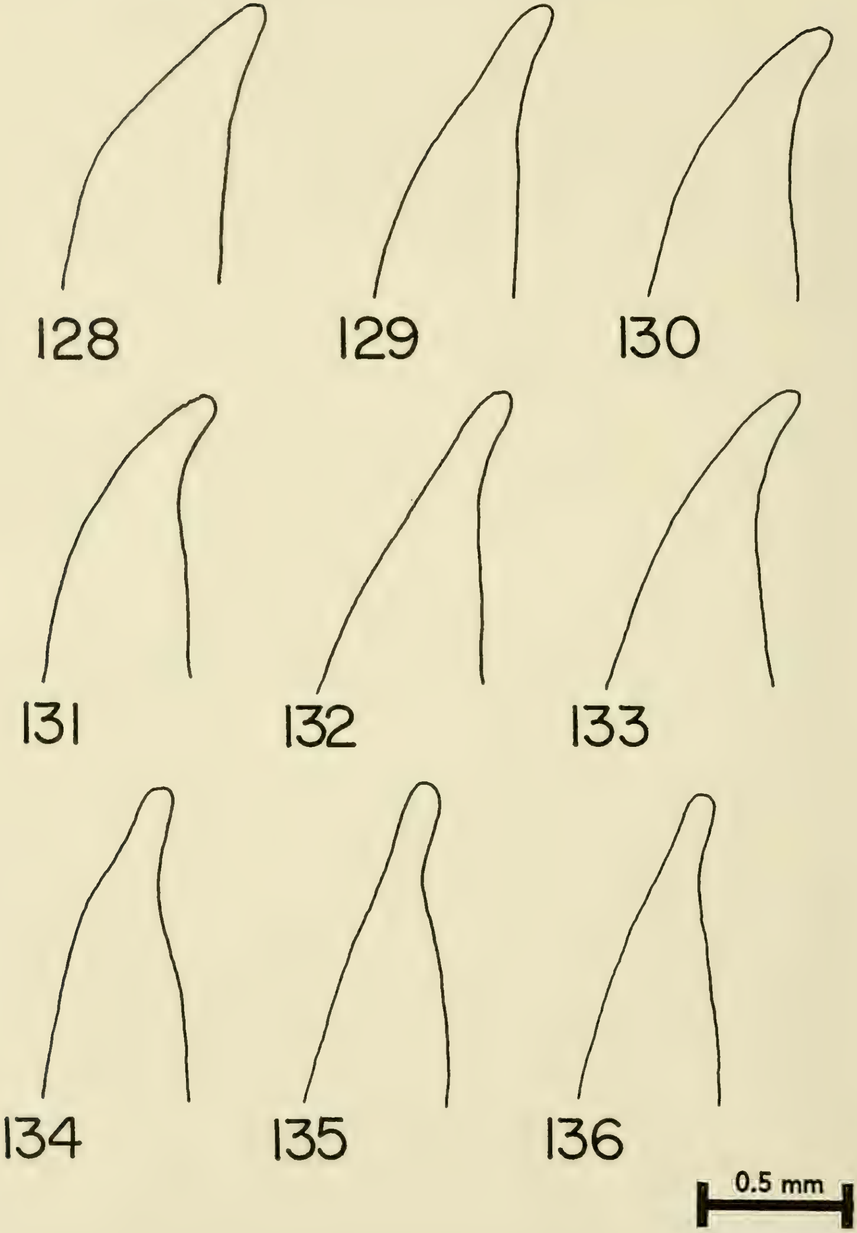
126 127

Figs. 126-127. Vectors for the six characters of males (Fig. 126) and females (Fig. 127) of *C. fulgida* for the first two discriminant functions. Each vector shows the change in the discriminant function that the corresponding character would produce if it varied independently. Units are same as in Figs. 124-125.

localities are bright red to red-purple, with occasional red individuals having a green sheen. It is not known whether northern or western populations exhibit a seasonal change of color as was noted for those from the central United States (see section on post-emergence changes of the adult).

Because of its genitalic difference, nearly uniform dark color, and its isolated geographic location, *C. f. westbournei* will be retained as a poorly differentiated subspecies, at least for the present. The populations of small individuals with quite variable color in Saskatchewan, northeastern Montana, and northern North Dakota could be considered as intermediates (Fig. 121).

Specimens with the markings wide and connected (particularly the apex of the humeral lunule and transverse portion of the middle band) are found in scattered localities in the northern and western parts of the range of the species: all Canadian localities, eastern Montana, northern North Dakota, Wyoming, south-central Colorado, and central New Mexico. Especially widely maculate individuals are found in populations from Carbon County, Wyoming, and Torrance County, New Mexico (locality 15 in the statistical analysis). This form was named *pseudowillistoni* by W. Horn, but because of its scattered and nonuniform distribution (it could be called polytopic), it is best not recognized as a subspecies.



FIGS. 128-136. Apex of aedeagus (dorsal aspect) of *C. fulgida* from various localities: Westbourne, Manitoba (FIG. 128); near Blucher, Saskatchewan (FIG. 129); Onefour, Alberta (FIG. 130); near Bottineau, North Dakota (FIG. 131); Oliver County, North Dakota (FIG. 132); Rawlins, Wyoming (FIG. 133); 4 miles northwest of Jamestown, Kansas (FIG. 134); 2.5 miles southwest of Plainview, Oklahoma (FIG. 135); 4 miles southeast of Willard, New Mexico (FIG. 136).

The closest relative of *C. fulgida* is *C. parowana*, which is found in the Great Basin, western Oregon, western Washington, and southern British Columbia. Except for a longer labrum and several differences of the male genitalia, it is quite similar to *C. fulgida* in general appearance and range of variation of color and maculation. Quite clearly, they evolved from a common ancestor that was probably widespread in the western United States and Canada in late Tertiary times. The rising mountains of the Cascadian Revolution apparently separated it into populations which became differentiated into the two modern species. *C. fulgida* is basically a species of cool climates; however, Pleistocene glaciers and the accompanying shift of climatic zones no doubt drove it south. As climates warmed and it moved northward again, relict populations were left in Arizona, New Mexico, and Texas (the locality of Woodward, Texas, listed as a doubtful locality earlier, may actually be a relict population in south-central Texas). The occurrence of dark individuals at Lincoln, Nebraska, a characteristic of more northern populations, may be explained by assuming that the species was not exterminated from there by the later glaciations and became dark due to the cool climate of that time.

C. macra

This species occurs between the Rocky and Appalachian Mountains (Fig. 137). Its distribution by counties or states is as follows:

MICHIGAN: Berrien, Emmet, Leelanau; WISCONSIN: Dane, St. Croix, Waushara, Wood; MINNESOTA: Ramsey, Scott, Wabasha, Washington; OHIO; INDIANA: Greene, Lake, Monroe, Porter, Posey, Putnam, Vigo; KENTUCKY: Henderson; TENNESSEE; ILLINOIS: Calhoun, Carroll, Cook, Mason, Morgan, Ogle, Whiteside; IOWA: Alexander, Benton, Blackhawk, Boone, Clinton, Des Moines, Johnson, Lee, Linn, Louisa, Monona, Pottawatamie, Van Buren, Woodbury; MISSOURI: Atchison, Clay or Jackson, Holt; ARKANSAS: Craighead, Crawford; LOUISIANA; TEXAS: Childress, Dallas, Denton, Eastland, Grayson, Hall, Hardeman, Hemphill, Kaufman, Montague, Potter, Randall, Stonewall, Wichita, Wilbarger; OKLAHOMA: Alfalfa, Beaver, Beckham, Caddo, Choctaw, Cimarron, Cleveland, Comanche, Cotton, Custer, Dewey, Ellis, Greer, Harmon, Harper, Hughes, Jackson, Johnston, Kingfisher, Kiowa, Logan, Love, Major, Marshall, McClain, Osage-Payne Co. line, Payne, Pontotoc, Roger Mills, Seminole, Texas, Woods, Woodward; KANSAS: Barber, Barton, Cheyenne, Clark, Clay, Comanche, Cowley, Douglas, Ellsworth, Kearney, Kiowa, Leavenworth, McPherson, Meade, Mitchell, Ness, Osbourne, Phillips, Pottawatomie, Reno, Riley, Rooks, Russell, Sedgwick, Shawnee, Stafford, Sumner, Trego; COLORADO: Denver, Larimer; WYOMING: Carbon; NEBRASKA: Brown, Buffalo, Cass, Chase, Cherry, Dakota, Dixon, Douglas, Dundy, Franklin, Hamilton, Lancaster, Madison, Merrick, Otoe, Platte, Saunders, Thomas; SOUTH DAKOTA: Brookings, Clay, Union. Towns that could not be located: Pine, Indiana; Adams and Herrold, Iowa. *Doubtful records:* Shoshone, Inyo County, California; Las Cruces, Dona Ana County; Socorro, Socorro County; and Albuquerque, Bernalillo County, New Mexico.

This species could be considered a sibling to *C. cuprascens* and *C. puritana* (see Table 18 for a comparison of the three), and they have been confused in the past, leading to erroneous records in the literature and misidentified specimens in museum collections. The ranges of *C. macra* and *C. cuprascens* overlap broadly, but there are notable areas of nonoverlaping; for example, *C. macra* is rare northwest of South Dakota and Wyoming, but *C. cuprascens*

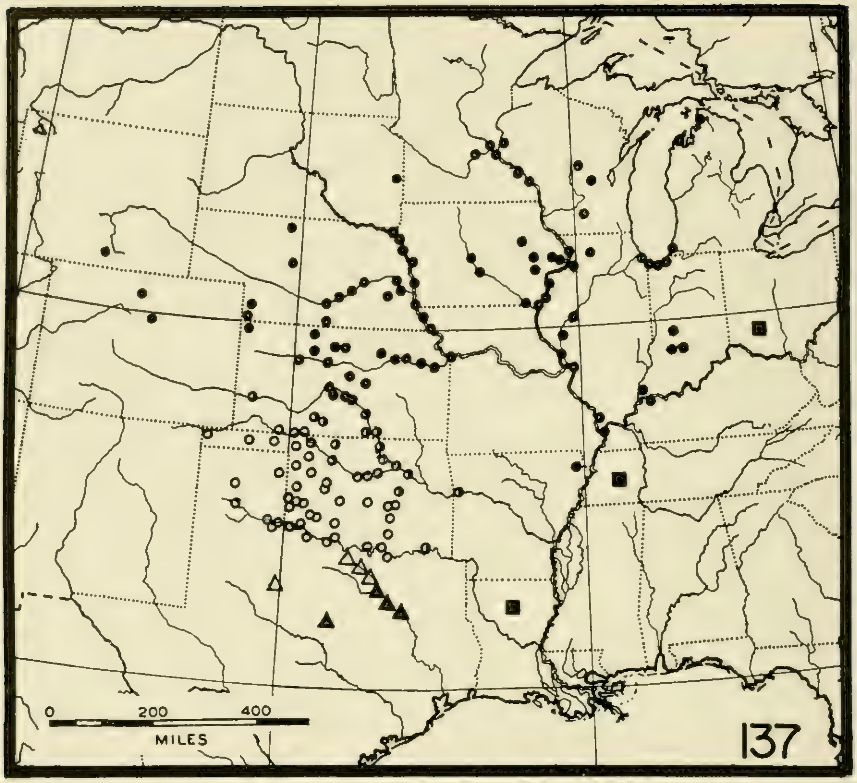


FIG. 137. Known distribution of *C. macra.* Shaded circle=*C. m. macra*, open circle=*C. m. fluviatilis*, half-shaded circle=intergrade population between *C. m. macra* and *C. m. fluviatilis*, shaded triangle=*C. m. amplicata*, open triangle=intergrade population between *C. m. fluviatilis* and *C. m. amplicata*, square=state record.

occurs as far north as Manitoba and Montana; *C. cuprascens* is absent from Michigan, where *C. macra* occurs; finally, *C. macra* does not occur in Alabama or Georgia, where *C. cuprascens* has been found. These two species also occupy the same ecological microhabitat; I have often seen them running together on the same sandbar. Nevertheless, out of dozens of mating pairs that I have collected, none involved two individuals of the wrong species. Also, no specimens that appear to be hybrids have been seen. Thus, I have no doubt that these forms are specifically distinct and genetically separate.

The following forms have been described within this species:

Cicindela macra Leconte, 1860. Type locality: Wisconsin and Minnesota (types bear yellow paper circles, signifying "Illinois, Missouri, and Central Valley").
Cicindela macra mercurialis Casey, 1913. Type locality: Iowa.
Cicindela macra topeka Casey, 1916. Type locality: Mt. Hope, Kansas.

Cicindela macra fluviatilis Vaurie, 1951. Type locality: Red River, north of Quanah, Hardeman County, Texas.
Cicindela macra amplicata Vaurie, 1951. Type locality: Denton County, Texas.

In recent years, three subspecies have been recognized: *C. m. macra*, the smallest dark green or green-brown form found north and east of Oklahoma; *C. m. fluviatilis*, the large, reddish, widely maculate form in Oklahoma and northwestern Texas; and *C. m. amplicata*, the large, dark green, narrowly maculate form in north-central Texas.

The following characters were measured in the study of geographic variation: (1) length of left elytron; (2) width of left elytron; (3) width of labrum; (4) length of labrum, including tooth; (5) width of middle band at a specified place (Fig. 114); (6) width of head; (7) shape of apex of middle band in arbitrary units (Fig. 115); (8) color of elytra, using color wheel.

TABLE 29. Localities and sample sizes of the specimens of *C. macra* measured.

Locality	N ♂	N ♀
1. INDIANA, Monroe Co., Bloomington	5	9
2. MINNESOTA, Wabasha Co., Dumfries; Scott Co., Jordan; Washington Co., Gray Cloud Island; WISCONSIN, St. Croix Co., North Hudson	12	10
3. IOWA, Woodbury Co., Sergeant Bluff	12	11
4. KANSAS, Ellsworth Co., Kanopolis Lake, s.e. Ellsworth Co.	12	11
5. KANSAS, Sumner Co., just n. of Geuda Springs	12	12
6. OKLAHOMA, Alfalfa Co., 3 mi. n., 5 e. of Cherokee	12	12
7. OKLAHOMA, Cleveland Co.	12	12
8. OKLAHOMA, Marshall Co., Lake Texoma State Park	12	9
9. TEXAS, Montague Co., Forestburg	12	8

Specimens from nine localities were measured; the localities and sample sizes are given in Table 29. Sample sizes were adequate from nearly all localities; however, specimens from Minnesota and Wisconsin were lumped into one sample.

The means for the characters and localities are given in Tables 30 and 31. Analyses of variance of the individual characters showed that there are significant differences ($p < 0.01$) among the means of all characters for both sexes (except characters 1 and 7 for males, which are significant at the 5% level). Pooled within-locality variance-covariance matrices are given in Tables 32 and 33. The sums of the among-locality variance components are 54.793 for males and 62.362 for females. The first two components for males and the first three for females are highly significant ($p < 0.01$), and the fourth for females is significant at the 5% level. The first three functions account for 95.31% of the variance (among localities relative to that within)

TABLE 30. Means of nine localities (see Table 29) and seven characters for males of *C. macra*. Values for characters 1-6 are in mm.

				Character			
Locality	1	2	3	4	5	6	7
1	8.09	2.04	1.60	0.71	0.45	3.04	4.60
2	7.89	2.01	1.56	0.67	0.33	3.03	3.52
3	8.08	2.02	1.61	0.69	0.39	3.09	3.72
4	8.09	2.09	1.63	0.70	0.39	3.14	4.08
5	8.27	2.12	1.67	0.74	0.47	3.20	3.86
6	8.18	2.11	1.69	0.74	0.55	3.26	3.92
7	8.17	2.11	1.69	0.72	0.71	3.29	3.92
8	8.12	2.09	1.69	0.73	0.70	3.23	3.64
9	8.42	2.27	1.75	0.78	0.42	3.37	3.41

TABLE 31. Means of nine localities (see Table 29) and seven characters for females of *C. macra*. Values for characters 1-6 are in mm.

				Character			
Locality	1	2	3	4	5	6	7
1	8.20	2.04	1.64	0.66	0.37	3.17	3.76
2	7.79	1.95	1.54	0.60	0.30	3.03	3.21
3	8.33	2.05	1.64	0.67	0.35	3.24	3.93
4	8.36	2.11	1.68	0.70	0.46	3.35	3.75
5	8.54	2.15	1.75	0.73	0.41	3.42	3.51
6	8.78	2.31	1.78	0.77	0.60	3.53	3.60
7	8.66	2.25	1.77	0.73	0.59	3.54	4.18
8	8.77	2.30	1.81	0.74	0.58	3.54	4.10
9	9.04	2.43	1.83	0.77	0.41	3.65	3.44

TABLE 32. Pooled within-locality variance-covariance matrix for males of *C. macra*. Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "1104"=0.1104.

					Character			
		1	2	3	4	5	6	7
Character	1	1104	230	171	75	40	280	412
	2		71	40	21	3	66	117
	3			46	20	2	61	59
	4				24	2	33	39
	5					124	6	79
	6						120	144
	7							4337

Table 33. Pooled within-locality variance covariance matrix for females of *C. macra.* Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "1076"=0.1076.

	Character						
Character	1	2	3	4	5	6	7
1	1076	226	187	104	72	365	217
2		81	43	29	16	82	47
3			55	23	16	76	36
4				26	0	43	66
5					102	11	64
6						174	70
7							4406

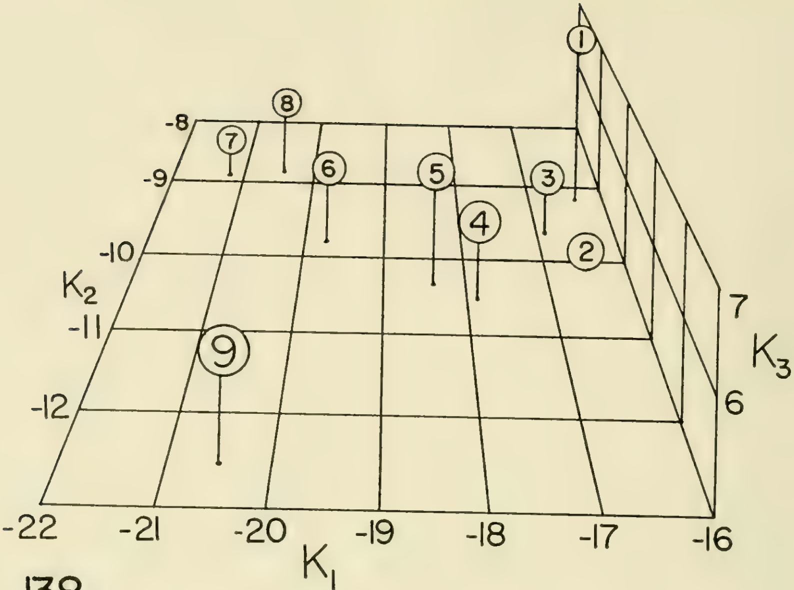
in males and 92.86% in females. The distributions of the means in the first three discriminant functions are shown in Figures 138 and 139 (however, the third function is not significant in males and could be ignored). Locality 9 is widely separated from the others, which form an elongate, loose cluster in males and three more compact clusters in females.

The results of the simultaneous testing procedure show that all combinations of pairs of means are significantly different at the 5% level except 1 vs. 3, 4 vs. 5, and 7 vs. 8 in both sexes; 2 vs. 3 in males; and 1 vs. 2, 6 vs. 7, and 6 vs. 8 in females.

Sets of vectors (Figs. 140 and 141), plotted in the first two functions, show geographic trends of the seven characters when compared with Figures 138 and 139. Specimens from locality 9 have relatively wider and shorter elytra. Specimens from the northeastern localities have relatively long, narrow elytra and long labra. Specimens from Oklahoma have wide heads and broad middle bands.

The results of the color analysis are shown in Fig. 142. Populations from north and east of Oklahoma consist mostly of dark green to dark red-green to dark reddish (actually brown) individuals. Populations from Oklahoma consist of mostly brighter red individuals, with fewer red-green and green individuals. The Texas population is similar to the northeastern populations in color.

These analyses confirm the existence of the three recognized subspecies. Locality 9, representing *C. m. amplicata*, is greatly different from all others. Localities 1-5 *(C. m. macra)* are significantly different from localities 6-8 *(C. m. fluviatilis)*. The inclusion of samples from other areas would no doubt fill in the gaps between the clusters in Figures 138 and 139. However, study of specimens from most of the localities in Figure 137 indicates that the variation within this species is in the form of a stepped cline, with narrow zones of intergradation between the three subspecies. In fact, three of the



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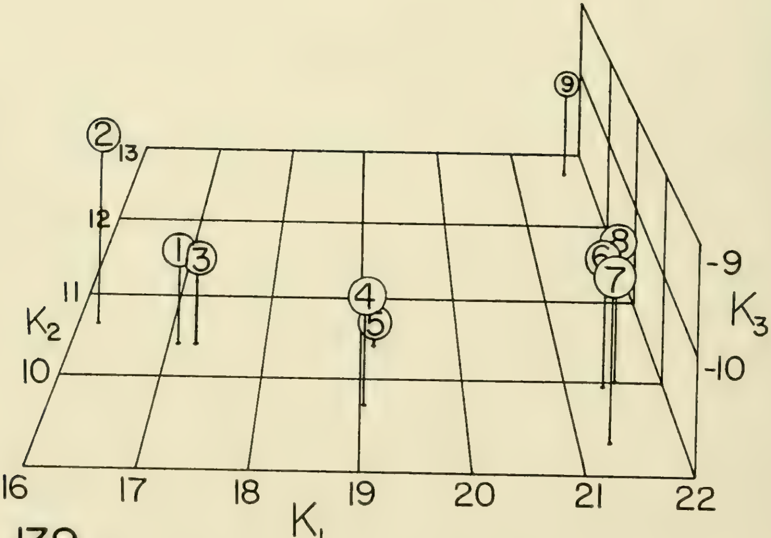

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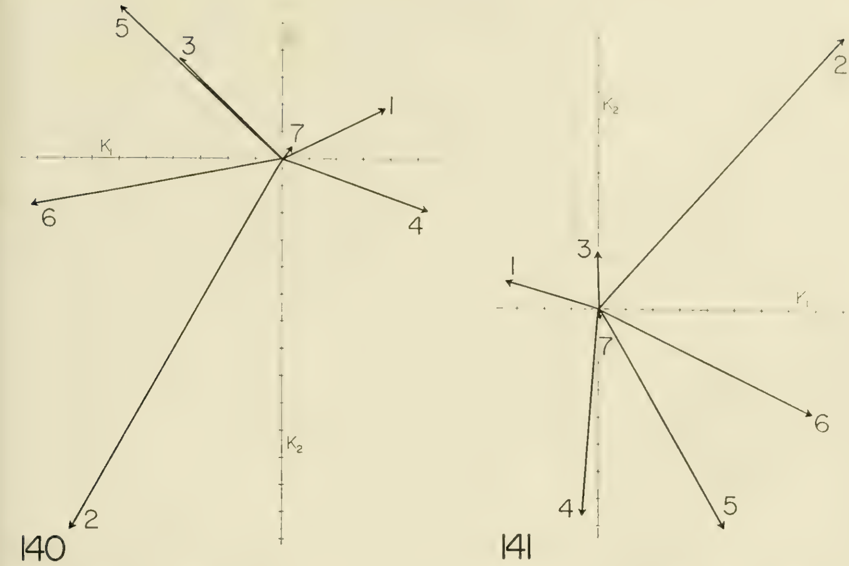
FIGS. 138-139. Distributions of the means of the nine localities for males (Fig 138) and females (Fig. 139) of *C. macra* in the first three discriminant functions (K_1, K_2, K_3), drawn as three-dimensional models, with numbered balls representing the means and vertical supports arising from the K_1, K_2 surface. Different sized balls indicate different distances from the viewer. The models are viewed from opposite directions, relative to the clusters.



Figs. 140-141. Vectors for the seven characters of males (Fig. 140) and females (Fig. 141) of *C. macra* for the first two discriminant functions. Each vector shows the change in the discriminant function that the corresponding character would produce if it varied independently. Units are same as in Figs. 138-139.

localities analyzed (5, 6, and 9) are in intergradation zones. Intergrade populations are characterized by much variability in color and maculation.

The fact that *C. macra* shows a greater differentiation into geographical races than does *C. cuprascens* might indicate that it has been in its present range (at least in the southern parts) for a longer time than *C. cuprascens*. If true, this also supports the idea that the two evolved on opposite sides of the Mississippi valley, as mentioned under *C. cuprascens*. The pattern of color variation of *C. macra* shows very clearly the effect of selection to match the substrate color. The limits of the reddish *C. m. fluviatilis* coincide almost exactly with the northeastern limits of red soil (Figs. 137 and 108). Populations intermediate between it and *C. m. macra* in southern Kansas, northeastern Oklahoma, and western Arkansas contain some reddish, some brown, and some green individuals. The area of occurrence of "true" *C. m. amplicata* possesses dark soil; however, in the northern and western parts of the range of this form, tan or reddish soils begin to appear, and populations contain many reddish and brown individuals.

This species is reported in the literature from three localities along the Rio Grande in New Mexico. No specimens have been seen from these localities, and they have been listed as doubtful. It is hard to imagine how the species could have gotten there.

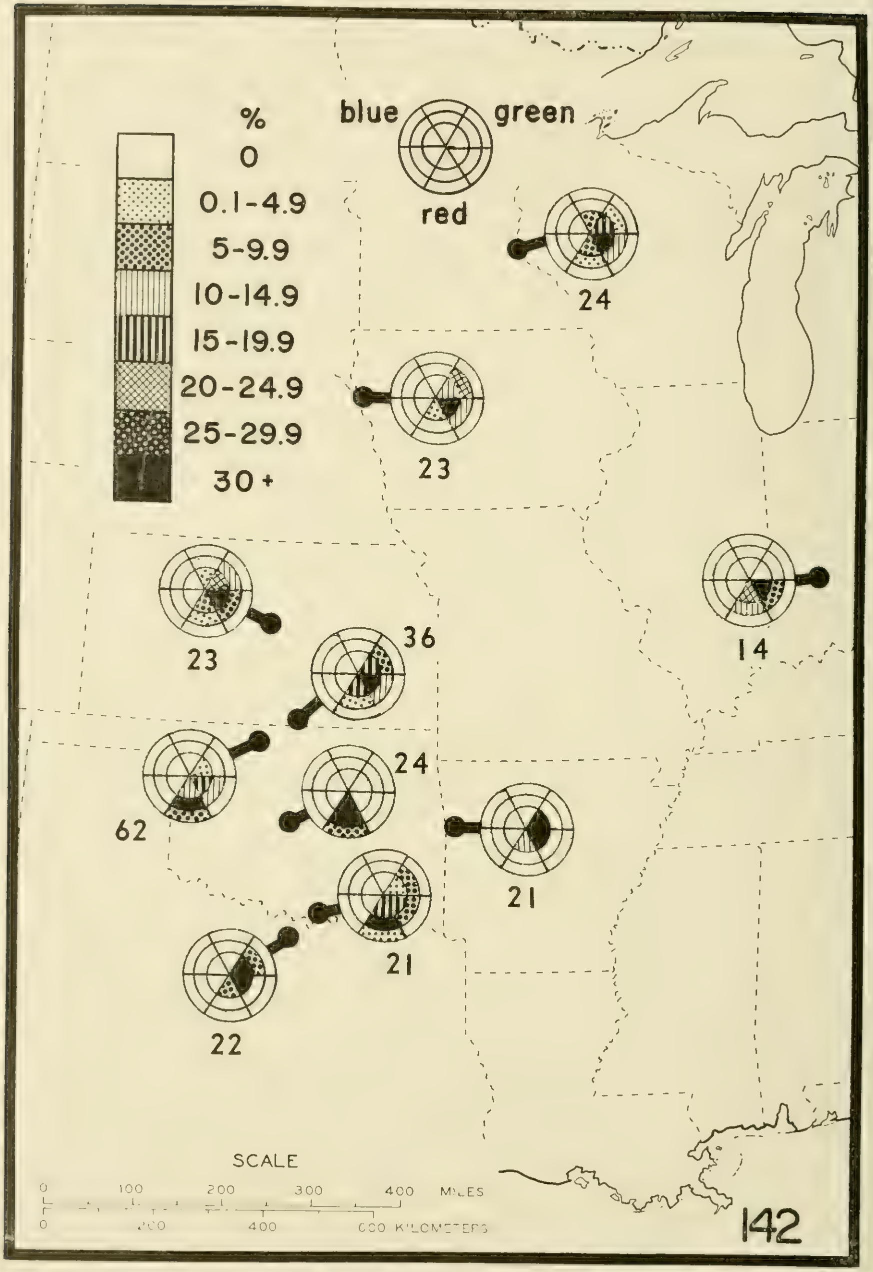

%
0
0.1-4.9
5-9.9
10-14.9
15-19.9
20-24.9
25-29.9
30+
blue
green
red
24
23
14
23
36
62
24
21
21
22
SCALE
0 100 200 300 400 MILES
0 200 400 600 KILOMETERS
142

FIG. 142. Results of color analysis of *C. macra* using the color wheel. Different degrees of shading indicate different percentages of the sample. The positions of the three major colors are shown at top center. Numbers show the sample size for each locality.

C. nevadica

This is a western species, occurring from the Mojave Desert in California and Sonora, Mexico, to the western edge of the Central Plains (Fig. 143). Its distribution by counties or states is as follows:

ALBERTA; SASKATCHEWAN; MANITOBA; MONTANA: Hill, Prairie, Roosevelt, Sheridan, Yellowstone; NORTH DAKOTA: Pierce, Ramsey; SOUTH DAKOTA: Hand;

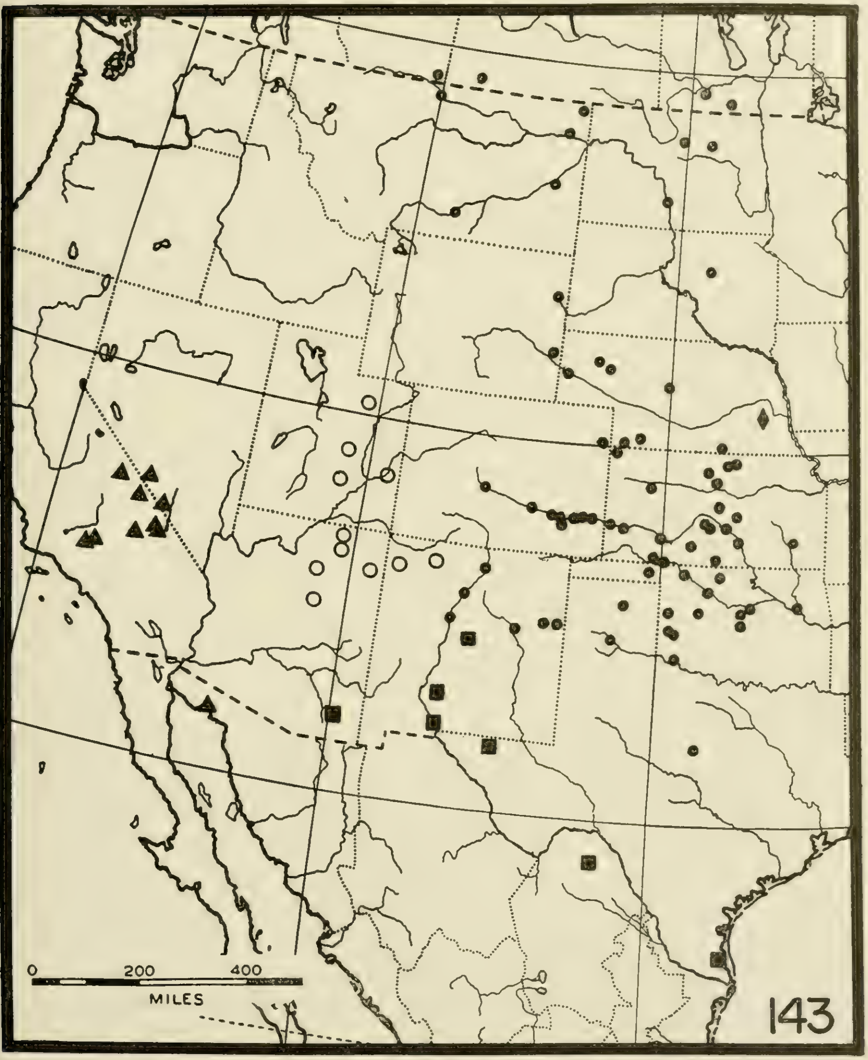


Fig. 143. Known distribution of *C. nevadica*. Triangle=*C. n. nevadica*, open circle=*C. n. tubensis*, shaded circle=*C. n. knausi*, square=*C. n. olmosa*, diamond=*C. n. lincolniana*.

WYOMING: Goshen, Weston; NEBRASKA: Dundy, Hitchcock, Lancaster, Nuckolls, Scotts Bluff, Sheridan; COLORADO: Bent, Chaffee, Prowers, Otero; KANSAS: Barber, Cheyenne, Clark, Cloud, Ellsworth, Ford, Gove, Hamilton, Kearney, Kiowa, Lincoln, McPherson, Meade, Mitchell, Reno, Republic, Russell, Sedgwick, Stafford, Sumner; OKLAHOMA: Alfalfa, Beaver, Beckham, Custer, Jackson, Logan, Major, Oklahoma, Payne, Roger Hills, Tulsa, Woods; TEXAS: Eastland, Hudspeth, Hutchinson, Kenedy, Randall; NEW MEXICO: Bernalillo, Dona Ana, Guadalupe, Quay, Rio Arriba, San Doval, San Juan, Santa Fe, Sierra, Taos, Torrance; UTAH: Duchesne, Emery, Moab, Wayne; ARIZONA: Apache, Cochise, Coconino, Navajo; NEVADA: Nye; CALIFORNIA: Inyo, Kern, San Bernadino; SONORA; COAHUILA. The exact location of Acnegas, Coahuila, Mexico, could not be found.

The following forms have been described within this species:

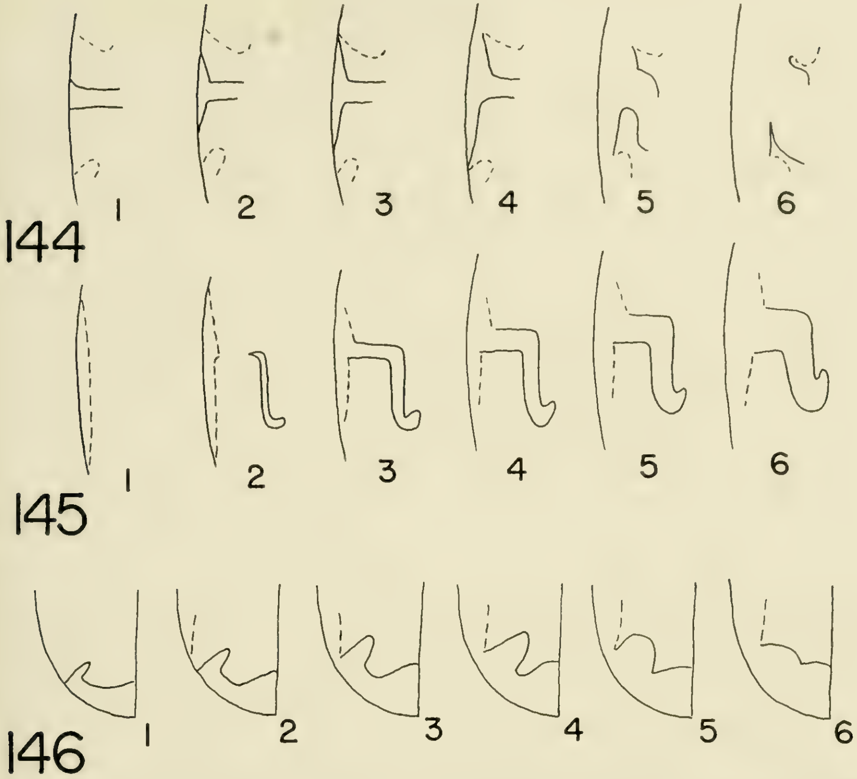
Cicindela nevadica Leconte, 1875c. Type locality: Nevada.
Cicindela Knausii Leng, 1902. Type locality: Kackley, Belvidere, and Great Spirit Springs, Kansas.
Cicindela lincolniana Casey, 1916. Type locality: Lincoln, Nebraska.
Cicindela nevadica tubensis Cazier, 1939. Type locality: Tuba City, Coconino County, Arizona.
Cicindela nenadica olmosa Vaurie, 1951. Type locality: Los Olmos, Kenedy County, Texas.

In recent years, all five of the above forms have been recognized as subspecies, *C. n. nevadica* being characterized by dark brown or green-brown color and often a reduced marginal line; *C. n. tubensis* by reddish color and often expanded markings; *C. n. olmosa* by dark greenish brown color and expanded markings; *C. n. knausi* by reddish brown, greenish brown, green, or blue color and average markings; and *C. n. lincolniana* by dark greenish brown color and reduced markings.

In the study of geographic variation, the following characters were measured: (1) length of left elytron; (2) width of left elytron; (3) width of labrum; (4) length of labrum, including tooth; (5) shape of base of middle band in arbitrary units (Fig. 144); (6) width of middle band in arbitrary units (Fig. 145); (7) width of apical lunule in arbitrary units (Fig. 146); (8) color of elytra, using color wheel.

Specimens from 18 localities were measured; the localities and sample sizes are given in Table 34. Sample sizes were adequate for nearly all localities, except some in New Mexico, Utah, and Kansas.

The means for the characters and localities are given in Tables 35 and 36. Analyses of variance of the individual characters showed that there are significant differences among the means of characters 3-7 ($p < 0.01$), and character 1 ($p < 0.05$); the means of character 2 are nonsignificant for both sexes. Pooled within-locality variance-covariance matrices are given in Tables 37 and 38. The sums of the among-locality variance components are 150.835 for males and 129.146 for females. The first four components are highly significant ($p < 0.01$); and the fifth is significant at the 5% level. The first three functions account for 95.67% of the variance (among localities relative to that within) in males and 93.15% in females. The distributions of the means in the first three discriminant functions are shown in Figures 147 and 148. Localities 1, 3-11, and 18 form a fairly compact cluster, while the other localities are scattered about to varying degrees.



Figs. 144-146. Illustrations of certain characters measured on elytra of *C. nevadica*; Fig. 144, arbitrary units for shapes of base of middle band; Fig. 145, arbitrary units for width of middle band; Fig. 146, arbitrary units for width of apical lunule.

The results of the simultaneous testing procedure show that all combinations of pairs of means are significantly different at the 5% level except 3 vs. 8, 4 vs. 7, 4 vs. 8, 4 vs. 9, 4 vs. 10, 4 vs. 11, 5 vs. 8, 8 vs. 10, 9 vs. 11, 10 vs. 11, and 12 vs. 13 for both sexes; 4 vs. 10, 5 vs. 7, 5 vs. 10, 7 vs. 10, 9 vs. 10, and 12 vs. 15 for males; and 1 vs. 9, 3 vs. 4, 3 vs. 5, 3 vs. 7, 3 vs. 8, 3 vs. 9, 3 vs. 10, 3 vs. 11, 3 vs. 13, 7 vs. 8, 7 vs. 9, and 8 vs. 9 for females. Thus, most members of the cluster are not different from one another, but the scattered means are usually significantly different from one another and from the cluster.

Sets of vectors (Figs. 149 and 150), plotted for the first two functions, show geographic trends of the seven characters when compared with Figures 147 and 148. Specimens with high values in K_1 have a wide base of the middle band, long labrum (in males), and narrow elytra (in females); and vice versa for specimens low in K_1.

The results of the color analysis are shown in Figure 151. Specimens from California and Nevada are predominantly dark reddish (appear brown) to

TABLE 34. Localities and sample sizes of the specimens of *C. nevadica* measured.

Locality	N	
	♂	♀
1. MANITOBA, 6 mi. s. of Hilton	10	10
2. NEBRASKA, Lancaster Co., Lincoln (west edge)	12	12
3. KANSAS, Lincoln Co., 11 mi. n., ½ mi. e. of Lincoln	9	5
4. KANSAS, McPherson, 1.5 mi. e. of Galva	12	12
5. KANSAS, Stafford Co., 11 mi. n.e. of Hudson	12	12
6. KANSAS, Clark Co., Englewood	12	12
7. COLORADO, Bent Co., Las Animas	12	12
8. OKLAHOMA, Alfalfa Co., 3 mi. e. of Cherokee	11	10
9. OKLAHOMA, Woods Co., 2.5 mi. s.w. of Plainview	12	12
10. TEXAS, Eastland Co., tank w. of Cisco	11	10
11. NEW MEXICO, Quay Co., 1 mi. n.e. of Tucumcari	12	12
12. NEW MEXICO, Taos Co., Ojo Caliente	3	4
13. NEW MEXICO, San Doval Co., 3 mi. w. of San Ysidro	4	9
14. ARIZONA, Navajo Co., 15 mi. n.n.w. of Kayenta	11	3
15. UTAH, Emery Co.	5	11
16. NEW MEXICO, Sierra Co., 25 mi. w. of Tularosa	12	8
17. NEVADA, Nye Co., Ash Meadows	12	8
18. CALIFORNIA, Kern Co., Saltdale	12	11

TABLE 35. Means of 18 localities (see Table 34) and seven characters for males of *C. nevadica*. Values for characters 1-4 are in mm.

Locality	Character						
	1	2	3	4	5	6	7
1	7.13	2.04	1.53	0.65	4.16	4.25	2.86
2	7.07	2.02	1.45	0.63	3.72	2.50	1.93
3	7.12	2.07	1.49	0.63	4.09	3.42	2.20
4	6.94	1.98	1.43	0.61	4.04	4.24	2.99
5	7.09	2.03	1.45	0.63	4.05	4.07	2.84
6	6.82	1.94	1.43	0.61	4.08	4.66	3.94
7	6.98	2.05	1.43	0.62	4.03	4.08	3.34
8	6.92	2.01	1.44	0.61	4.05	4.08	2.40
9	7.06	2.02	1.47	0.60	4.08	4.57	3.18
10	6.94	2.03	1.44	0.61	4.14	4.32	2.95
11	6.96	2.01	1.45	0.60	4.12	4.56	3.41
12	7.19	2.08	1.49	0.71	4.23	4.60	3.57
13	7.07	2.01	1.45	0.69	4.10	4.38	3.28
14	6.57	1.92	1.39	0.64	5.19	5.88	5.66
15	6.74	1.99	1.43	0.66	4.32	5.14	4.42
16	6.94	1.99	1.40	0.62	4.35	5.48	5.28
17	7.19	2.03	1.51	0.60	1.42	4.23	1.94
18	6.86	1.98	1.41	0.59	3.98	5.18	3.89

TABLE 36. Means of 18 localities (see Table 34) and seven characters for females of *C. nevadica*. Values for characters 1-4 are in mm.

				Character			
Locality	1	2	3	4	5	6	7
1	7.86	2.32	1.65	0.68	4.11	3.89	2.69
2	7.50	2.25	1.51	0.59	3.39	2.60	1.68
3	7.63	2.27	1.51	0.64	4.12	4.18	2.90
4	7.63	2.27	1.54	0.64	4.10	3.97	2.93
5	7.45	2.30	1.56	0.66	4.00	3.61	2.81
6	7.48	2.21	1.53	0.64	4.10	4.53	3.62
7	7.34	2.21	1.50	0.62	4.09	3.88	2.71
8	7.61	2.23	1.54	0.62	4.10	3.96	2.79
9	7.55	2.22	1.54	0.64	4.12	4.03	2.71
10	7.50	2.23	1.50	0.61	4.13	4.63	3.06
11	7.74	2.26	1.55	0.64	4.13	4.13	2.76
12	7.97	2.28	1.57	0.71	4.25	4.48	3.90
13	7.40	2.14	1.51	0.65	4.11	4.22	3.33
14	7.30	2.20	1.52	0.66	5.37	6.20	6.10
15	7.45	2.22	1.54	0.68	4.25	5.05	3.81
16	7.65	2.23	1.49	0.65	4.44	5.18	5.49
17	7.60	2.25	1.57	0.62	1.41	1.00	1.91
18	7.38	2.23	1.50	0.59	3.98	4.88	3.56

TABLE 37. Pooled within-locality variance-covariance matrix for males of *C. nevadica*. Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "1187"=0.1187.

					Character			
		1	2	3	4	5	6	7
Character	1	1187	311	220	132	135	45	203
	2		108	64	39	38	29	60
	3			60	30	33	41	38
	4				24	15	22	34
	5					717	504	659
	6						2771	799
	7							3503

dark green. The Utah and Arizona samples are mostly reddish, and the northern New Mexico samples are similar, but contain many red-green individuals. The southern New Mexico population is dark red (brown) to dark-green. Other populations are quite variable in color and contain many individuals with brighter colors (in the south; northern populations are darker).

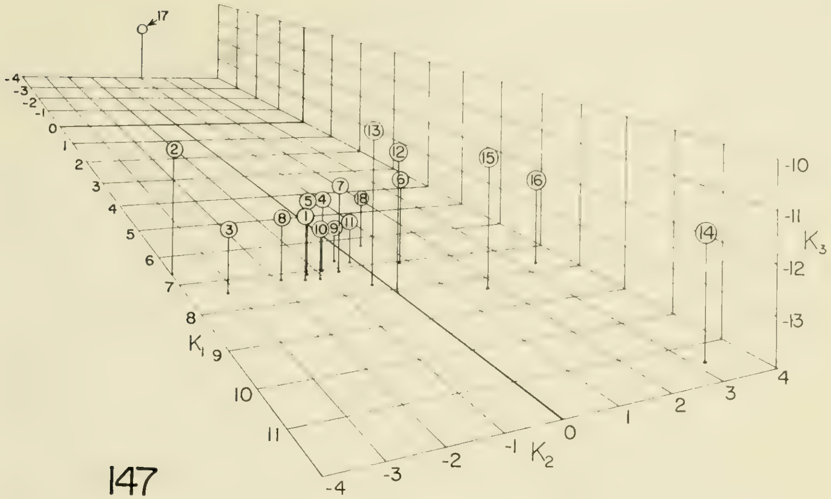
These analyses, in general, support the existence of the five subspecies. Samples representing *C. n. lincolniana* (2) and *C. n. olmosa* (16) are well

TABLE 38. Pooled within-locality variance-covariance matrix for females of *C. nevadica.* Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "1198"=0.1198.

					Character			
		1	2	3	4	5	6	7
Character	1	1198	316	215	117	60	167	—26
	2		121	65	35	32	61	—13
	3			61	24	14	33	—27
	4				23	15	25	9
	5					478	321	245
	6						2101	1040
	7							2876

separated from the others in the statistical analysis. The means of *C. n. knausi* (1, 3-13) form a compact cluster. The means of *C. n. tubensis* (14 and 15) are widely separated, apparently because sample 14 contained many small, very widely maculate individuals. Localities 12 and 13 could be called intermediates between *C. n. tubensis* and *C. n. knausi* on the basis of their color. The means of *C. n. nevadica* (17 and 18) are also widely separated because most individuals in sample 17 have no marginal line, while those in 18 do, causing them to resemble *C. n. knausi* (still, 18 is significantly different from all others). However, the geographical isolation of *C. n. nevadica* and its characteristic dark color and wide transverse portion of the middle band justify its recognition. Some of the Utah specimens of *C. n. tubensis* lack the red color typical of Arizona populations, being greenish brown and thus resembling *C. n. knausi*; however, their markings average much wider than those of *C. n. knausi.* The status of the population in southeastern Arizona (if it is a valid record) is in doubt (Fig. 143). The eight specimens from there are dark green to green-brown, and have average markings with a marginal line. At present, they are being called *C. n. olmosa.* The population of "*C. n. olmosa*" from central New Mexico may be intergrades between this subspecies and *C. n. knausi*; I have seen no specimens from there.

C. nevadica almost certainly evolved in the western United States, but its range is so large, it is impossible to guess where. Its closest relatives are *C. sperata* and *C. marutha*, found in the Great Basin, northern Mexico, southern Great Plains, and (*C. sperata* only) southern Texas. The three probably evolved as the rising western mountains in late Tertiary times isolated populations of a common ancestor. *C. nevadica* then probably became widespread in the Southwest during the early Pleistocene pluvial periods, when moist climates permitted easy dispersal. During drier interglacial periods, many populations were apparently extinguished and resulting complete or partial isolation favored the development of geographic races: *C. n.*



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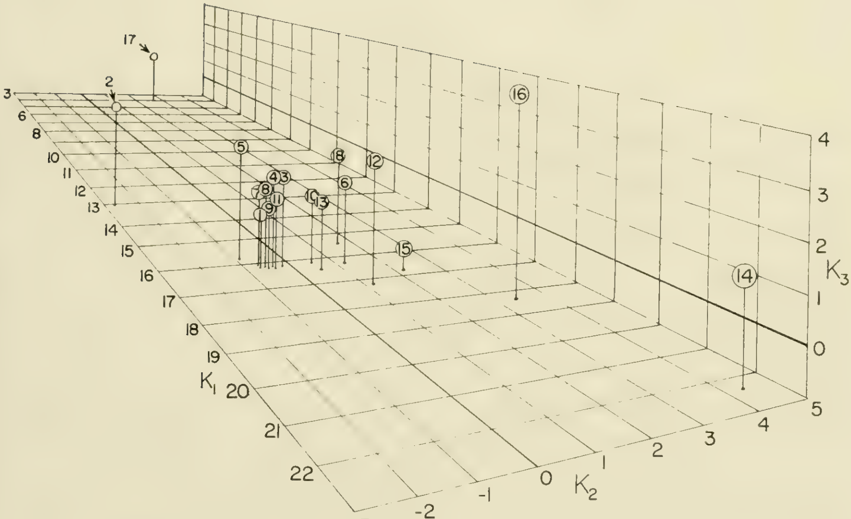

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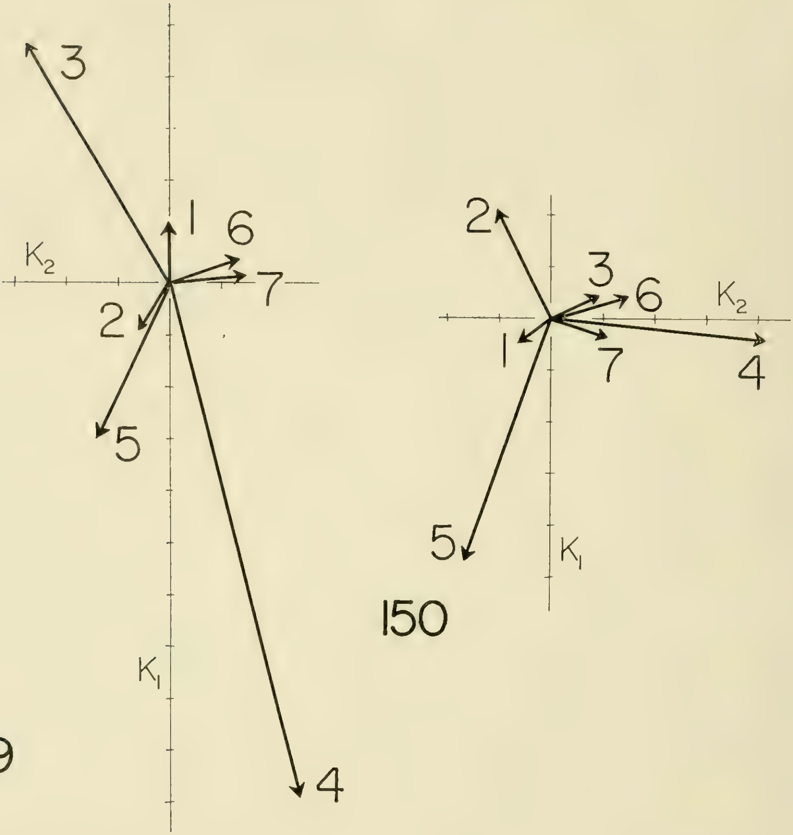
Figs. 147-148. Distributions of the means of the 18 localities for males (Fig. 147) and females (Fig. 148) of *C. nevadica* in the first three discriminant functions (K_1, K_2, K_3), drawn as three-dimensional models, with numbered balls representing the means and vertical supports arising from the K_1, K_2 surface. Different sized balls indicate different distances from the viewer.

nevadica in the western Great Basin and *C. n. tubensis* on the Colorado Plateau, where it developed a red dorsal color because of the red soils in that region (Fig. 108). A third form (or ancestors of *C. n. tubensis*) spread



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FIGS. 149-150. Vectors for the seven characters of males (Fig. 149) and females (Fig. 150) of *C. nevadica* for the first two discriminant functions. Each vector shows the change in the discriminant function that the corresponding character would produce if it varied independently. Units are same as in Figs. 147-148.

throughout the region drained by the Rio Grande and Pecos River; those along the lower Rio Grande became *C. n. olmosa*, while the others (*C. n. knausi*) dispersed northeastward. Glaciations evidently pushed *C. n. knausi* as far south as central Texas, where a relict population still exists in Eastland County. *C. n. knausi* probably reached the Lincoln, Nebraska, vicinity sometime after the Kansan glaciation, probably during the Yarmouth. From then on, it was apparently isolated from the rest of the gene pool and evolved into *C. n. lincolniana*. After the Wisconsin glaciation, *C. n. knausi* quickly dispersed northward into the Dakotas, Montana, and southern Canada. The fact that *C. n. knausi* has not developed completely reddish populations in western Oklahoma indicates that it has not been in this area as long as *C. n. tubensis* has been on the Colorado Plateau; however, the Oklahoma popula-

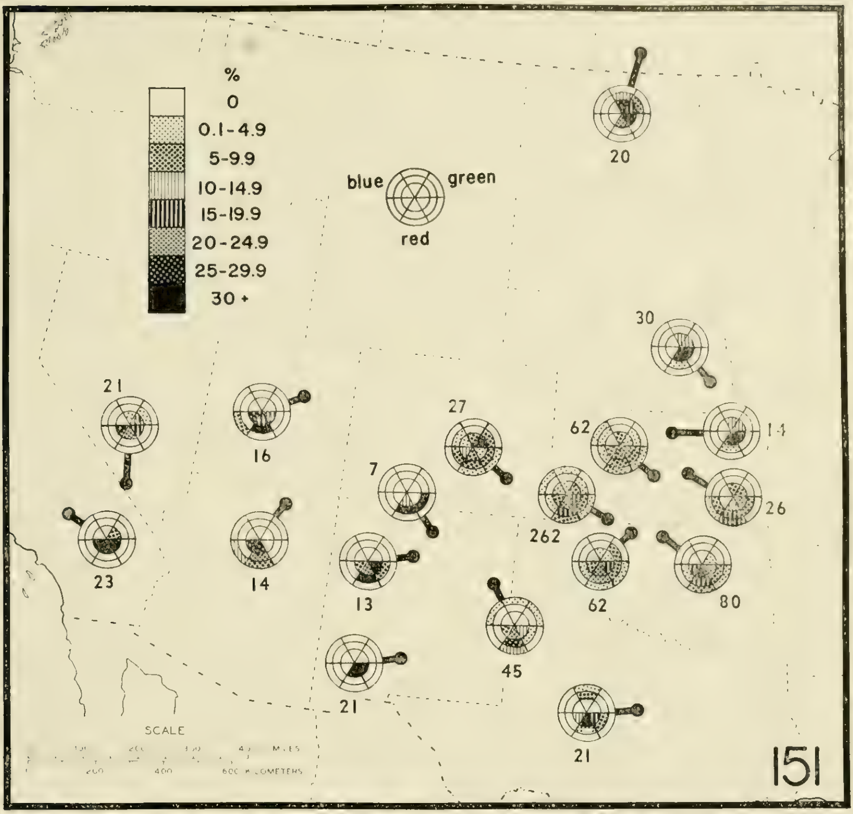


FIG. 151. Results of color analysis of *C. nevadica* using the color wheel. Different degrees of shading indicate different percentages of the sample. The positions of the three majors colors are shown at top center. Numbers show the sample size for each locality.

tions seem to be evolving in that direction, because they contain many bright red individuals, compared to populations from north of there (Fig. 151).

C. togata

This is a southern species found along the Gulf and Atlantic coasts from South Carolina to northern Mexico, and inland from western Texas to Nebraska (Fig. 152). Its distribution by counties or states is as follows:

NEBRASKA: Dodge, Fillmore, Lancaster, Nuckolls, Saunders; COLORADO: Chaffee, Otero; KANSAS: Barber, Butler, Clark, Cloud, Kiowa, Lincoln, McPherson, Mitchell, Reno, Republic, Sedgwick, Stafford; OKLAHOMA: Alfalfa, Beckham, Blaine, Garfield, Grant, Harmon, Harper, Jackson, Logan, Muskogee, Woods; NEW MEXICO: Chaves, Eddy, Guadalupe, Torrance; TEXAS: Andrews, Aransas, Bailey, Brazoria, Calhoun, Cameron, Childress, Dallas, Dawson, Dimmet, El Paso, Gaines, Galveston, Harris, Hidalgo, Hudspeth, Jackson, Jefferson, Kenedy, Kleberg, Live Oak, Matagorda, Mitchell, Nueces, Reeves, San Patricio, Val Verde, Wichita, Wilbarger; TAMAULIPAS; LOUISIANA: Cameron; ALABAMA: Mobile; FLOR-

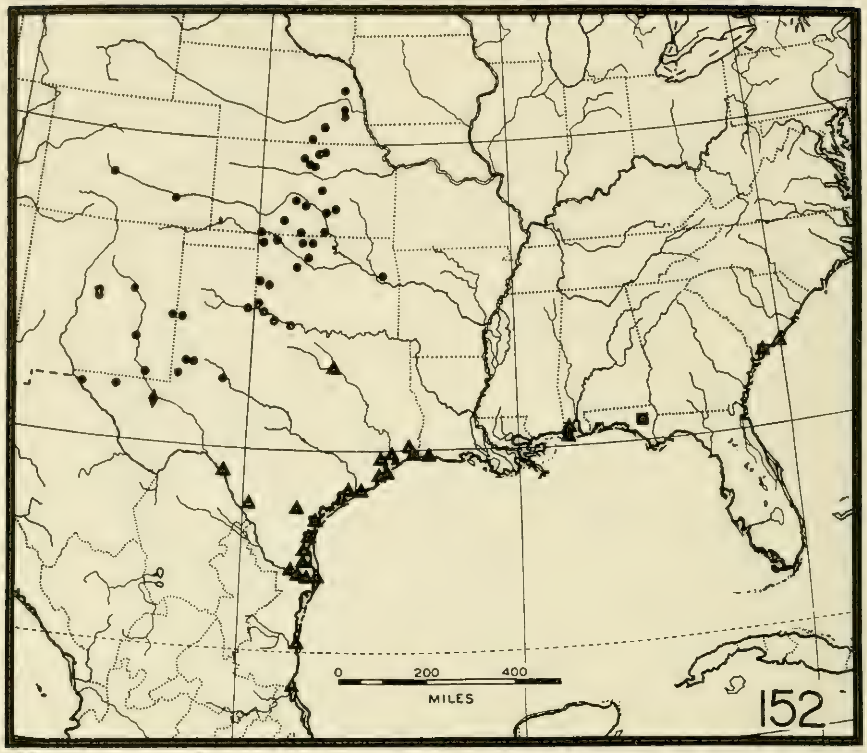


FIG. 152. Known distribution of *C. togata.* Triangle=*C. t. togata,* circle=*C. t. globicollis,* diamond=intergrade population, square=state record.

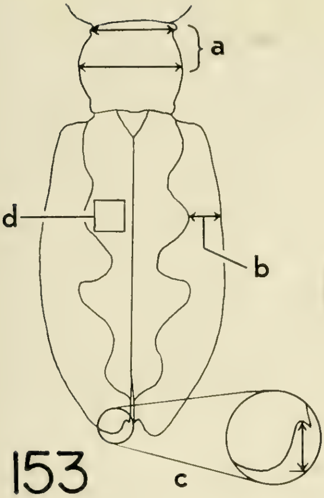
IDA; SOUTH CAROLINA: Beaufort, Charleston. The town of Meredith, South Carolina, could not be located. Saltair, Utah, is a doubtful record.

The following forms have been described within this species:

Cicindela togata LaFerté, 1841. Type locality: Texas.
Cicindela togata latilabris, new name for *Cicindela togata apicalis* W. Horn, 1897 (not *apicalis* Chaudoir, 1843). Type locality: Nebraska, Kackley (misspelled "Kakley"), Kansas. Preoccupied.
Cicindela globicollis Casey, 1913. Type locality: Clark County, Kansas.
Cicindela fascinans Casey, 1914. Type locality: Santa Rosa, New Mexico.

In recent years, three subspecies have been recognized: *C. t. togata,* the rather small coastal form with the apical elytral spine of the female greatly retracted; *C. t. globicollis,* the large northern form with the apical elytral spine of the female slightly retracted; and *C. t. fascinans,* the small southwestern form with expanded markings and slightly retracted apical elytral spine in the female.

The following characters were measured in the study of geographic variation: (1) width of head; (2) width of pronotum at widest point; (3)



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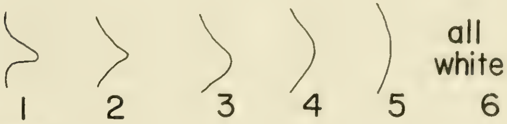

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Figs. 153-154. Illustrations of certain characters measured on *C. togata*; Fig. 153: a=pronotal bulge, b=width of maculation, c=retraction of elytral spine of female, d=number of punctures in 0.45 m^2 area at this position; Fig. 154, arbitrary units for shape of middle band.

"pronotal bulge," the difference between character 2 and the width of the pronotum at its anterior margin (Fig. 153a); (4) width of left elytron; (5) length of left elytron; (6) width of maculation at a specified place (Fig. 153b); (7) retraction of left apical elytral spine (distance from its base to apex of elytron) of female (Fig. 153c); not measurable in males because the spine is truly apical; (8) number of punctures in a 0.45 mm^2 square on a specified part of the left elytron (Fig. 153d); (9) average width of setae on center of pronotum; (10) shape of middle band in arbitrary units (Fig. 154); (11) color of elytra in arbitrary units: 1=dark green-brown, 2=dark green-cupreous, 3=green-cupreous, 4=cupreous, 5=dark purplish cupreous, 6=dark green-purple; (12) length of labrum, excluding tooth; (13) width of labrum.

Specimens from 19 localities were measured; the localities and sample sizes are given in Table 39. Sample sizes were adequate except for localities in the southwestern part of the range and from Dallas, Texas. Specimens from New Mexico were lumped into one sample.

The means for the characters and localities are given in Tables 40 and 41. Analyses of variance of the individual characters showed that there are significant differences ($p < 0.01$) among the means of all characters. Pooled within-locality variance-covariance matrices are given in Tables 42 and 43. The sums of the among-locality variance components are 258.487 for males and 284.879 for females. The first eight components for males and the first five for females are highly significant ($p < 0.01$), and the sixth component

Table 39. Localities and sample sizes of the specimens of *C. togata* measured.

Locality	N ♂	N ♀
1. NEBRASKA, Lancaster Co., Lincoln (west edge)	10	10
2. KANSAS, Republic Co., ½ mi. e., 1 s. of Talmo	10	10
3. KANSAS, Lincoln Co., 3 mi. w., 2 s. of Barnard	10	10
4. KANSAS, Butler Co., El Dorado (west edge)	10	10
5. KANSAS, Stafford Co., 11 mi. n.e. of Hudson	10	10
6. KANSAS, Clark Co., Englewood	10	10
7. OKLAHOMA, Alfalfa Co., 3 mi. e. of Cherokee	10	10
8. OKLAHOMA, Garfield Co., ½ mi. n.w. of Drummond	10	10
9. OKLAHOMA, Jackson Co., 3.5 mi. s. of Eldorado	10	10
10. TEXAS, Bailey Co., 9 mi. s., 9 w. of Muleshoe (Coyote L.); NEW MEXICO, Roosevelt Co., 4 mi. e., 1 s. of Arch	4	5
11. TEXAS, Andrews Co., 8 mi. n.w., 3.5 mi. s.w. of Andrews (Shafter L.)	9	10
12. NEW MEXICO, Chaves Co., 8 mi. n.e. of Roswell; Eddy Co., 6 mi. e., 2 n. of Loving	6	1
13. TEXAS, Hudspeth Co., 90 mi. e. of El Paso (near Salt Flat)	7	2
14. TEXAS, Val Verde Co., Del Rio	10	10
15. TEXAS, Dallas Co., Dallas	1	3
16. TEXAS, Kleberg Co., Riviera Beach	10	10
17. TEXAS, Galveston Co., Galveston	10	10
18. ALABAMA, Mobile Co., Coden	10	10
19. SOUTH CAROLINA, Charleston Co., Folly Beach	10	10

Table 40. Means of 19 localities (see Table 39) and 12 characters for males of *C. togata*. Values for characters 1-6, 9, 12, and 13 are in mm.

	Character 1	2	3	4	5	6	8	9	10	11	12	13
1	3.04	2.40	0.44	2.01	7.46	0.54	63.0	0.0190	1.29	1.25	0.76	1.47
2	3.21	2.44	0.43	2.04	7.51	0.59	60.1	0.0196	1.42	1.57	0.75	1.49
3	2.92	2.23	0.37	1.92	7.02	0.64	63.4	0.0180	2.34	2.42	0.74	1.37
4	3.09	2.41	0.44	2.02	7.39	0.66	57.8	0.0164	1.81	3.65	0.72	1.47
5	3.11	2.40	0.38	2.03	7.41	0.78	64.0	0.0200	2.77	3.06	0.74	1.47
6	2.93	2.25	0.40	1.90	6.78	0.77	60.1	0.0194	3.03	3.85	0.72	1.36
7	2.97	2.28	0.38	1.90	7.07	0.72	64.8	0.0190	2.53	4.19	0.69	1.41
8	3.09	2.36	0.43	2.00	7.37	0.71	56.2	0.0194	2.49	4.44	0.75	1.46
9	3.21	2.41	0.42	2.00	7.21	0.89	56.2	0.0210	3.35	4.40	0.75	1.47
10	3.10	2.42	0.38	1.96	7.26	0.83	54.2	0.0235	2.45	4.38	0.79	1.49
11	3.09	2.41	0.38	2.01	7.33	1.01	51.9	0.0227	4.01	4.30	0.79	1.53
12	2.72	2.01	0.32	1.69	6.40	0.81	63.3	0.0235	3.57	4.02	0.65	1.28
13	3.03	2.17	0.34	1.88	6.66	1.88	53.3	0.0239	6.00	4.14	0.79	1.37
14	2.95	2.17	0.36	1.86	6.77	0.62	55.5	0.0200	2.85	4.77	0.71	1.33
15	2.82	1.95	0.21	1.74	6.25	0.61	61.0	0.0220	3.60	4.60	0.65	1.26
16	3.10	2.29	0.40	1.95	6.86	0.72	55.1	0.0225	3.28	4.69	0.74	1.36
17	3.06	2.20	0.32	1.93	6.84	0.67	55.2	0.0191	2.77	4.80	0.72	1.35
18	2.83	1.96	0.27	1.81	6.38	0.70	54.7	0.0186	2.77	4.78	0.65	1.24
19	3.06	2.19	0.32	1.87	6.84	0.71	55.2	0.0175	1.51	4.89	0.72	1.34

Table 41. Means of 19 localities (see Table 39) and 13 characters for females of *C. togata*. Values for characters 1-7, 9, 12, and 13 are in mm.

	Character												
Locality	1	2	3	4	5	6	7	8	9	10	11	12	13
1	3.33	2.63	0.41	2.31	8.23	0.66	0.14	56.1	0.0188	1.17	1.53	0.80	1.60
2	3.49	2.63	0.38	2.31	8.25	0.59	0.16	55.4	0.0201	1.23	1.44	0.81	1.60
3	3.15	2.39	0.34	2.06	7.48	0.57	0.10	58.9	0.0172	1.41	2.32	0.71	1.44
4	3.24	2.45	0.38	2.12	7.57	0.62	0.13	53.3	0.0178	2.09	3.82	0.74	1.46
5	3.26	2.51	0.35	2.21	7.83	0.76	0.11	57.4	0.0208	2.38	2.83	0.78	1.55
6	3.07	2.32	0.36	2.05	7.08	0.75	0.11	59.9	0.0198	2.67	3.71	0.74	1.39
7	3.19	2.40	0.33	2.11	7.70	0.71	0.11	57.3	0.0193	1.97	3.61	0.76	1.49
8	3.43	2.59	0.40	2.24	8.01	0.70	0.18	50.9	0.0205	1.80	3.52	0.80	1.57
9	3.22	2.37	0.34	2.07	7.32	0.74	0.14	55.5	0.0210	2.07	4.41	0.75	1.45
10	3.36	2.61	0.41	2.33	7.99	0.87	0.14	50.8	0.0252	2.28	3.88	0.86	1.59
11	3.24	2.48	0.34	2.18	7.65	0.92	0.12	51.5	0.0213	3.16	3.88	0.82	1.58
12	3.38	2.51	0.36	2.20	7.89	1.18	0.10	54.0	0.0230	3.00	3.90	0.86	1.57
13	3.10	2.10	0.28	1.97	6.86	1.97	0.11	55.5	0.0240	6.00	4.20	0.83	1.35
14	3.29	2.37	0.33	2.11	7.31	0.68	0.39	51.8	0.0211	3.01	4.82	0.77	1.47
15	3.23	2.27	0.32	2.07	7.25	0.77	0.36	48.7	0.0207	3.07	4.70	0.73	1.38
16	3.30	2.42	0.34	2.08	7.33	0.74	0.42	49.2	0.0239	2.82	4.71	0.76	1.43
17	3.32	2.28	0.29	2.11	7.34	0.69	0.44	51.8	0.0197	1.70	4.96	0.77	1.45
18	3.08	2.13	0.27	2.01	6.80	0.75	0.30	50.5	0.0176	2.15	4.71	0.70	1.35
19	3.22	2.24	0.30	1.98	7.02	0.67	0.30	54.0	0.0176	1.37	4.87	0.75	1.39

Table 42. Pooled within-locality variance-covariance matrix for males of *C. togata*. Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "186"=0.0186.

		Character											
		1	2	3	4	5	6	8	9	10	11	12	13
Character	1	186	146	14	102	407	72	—2690	1	89	13	52	81
	2		156	32	91	375	70	—2773	0	129	18	47	72
	3			27	10	36	9	—344	0	28	—13	6	7
	4				93	294	53	—1957	0	91	31	36	51
	5					1345	193	—7617	1	315	100	141	213
	6						104	—1594	0	229	29	22	34
	8							228105	—9	—1602	—571	—1000	—1442
	9								0	1	—0	0	0
	10									3449	225	34	52
	11										1684	—3	22
	12											24	26
	13												47

for females is significant at the 5% level. The first three functions account for 87.95% of the variance (among localities relative to that within) in males and 88.96% in females. The distributions of the means in the first three discriminant functions are shown in Figures 155 and 156. Localities 14-19 form a fairly compact cluster, while the others are scattered in a loose cluster, except 13, which is widely separated.

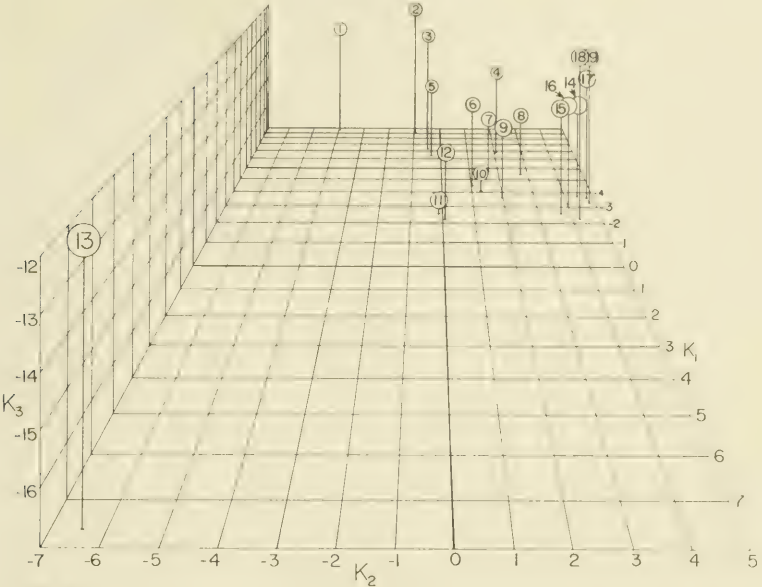
The results of the simultaneous testing procedure show that all combinations of pairs of means are significantly different at the 5% level except 15 vs. 16 and 15 vs. 18 for both sexes; 15 vs. 6, 15 vs. 9, 15 vs. 10, 15 vs. 12, 15 vs. 14, 15 vs. 17, and 15 vs. 19 for males; and 4 vs. 8, 5 vs. 7, 6 vs. 12, 9 vs. 12, 10 vs. 12, 11 vs. 12, and 14 vs. 15 for females. The low sample size of one individual for males from locality 15 and of females from locality 12 accounts for the many nonsignificant pairs involving those localities.

Sets of vectors (Figs. 157 and 158), plotted for the first two functions, show geographic trends of the characters when compared with Figures 155 and 156. Specimens with high values in K_1 (southwestern localities) have wide maculation, a long labrum, a greater pronotal bulge, and (in males) wider pronotal setae. Specimens low in K_1 and K_2 (northern localities) have a wide labrum, narrow head, and low arbitrary color values. Specimens low in K_1 and high in K_2 (coastal localities) have a wide head, a narrow labrum, high color values, and (in females) wide pronotal setae and a more greatly retracted elytral spine.

The pattern of variation of four of these characters is shown in Figure 159. The width of maculation shows a gradual increase from northeast to southwest, while all coastal and eastern Texas samples have narrow maculation. The same general pattern is shown by the width of pronotal setae, although some eastern Texas samples have very high values. Arbitrary color values increase from northeast to southwest, thence to the southeast. The retraction

TABLE 43. Pooled within-locality variance-covariance matrix for females of *C. togata*. Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "268"=0.0268.

		Character												
		1	2	3	4	5	6	7	8	9	10	11	12	13
Character	1	268	181	30	152	571	74	21	−2681	0	111	7	62	117
	2		202	49	120	439	59	8	−1858	1	104	−5	45	90
	3			38	21	72	6	−1	−7	0	−3	−21	7	14
	4				132	379	54	13	−2015	0	91	28	40	76
	5					1590	211	53	−7603	1	344	115	154	273
	6						94	12	−910	1	218	13	21	39
	7							18	−87	−0	26	8	7	9
	8								226118	−0	−2788	1153	−840	−1483
	9									0	1	−0	0	0
	10										2310	13	47	66
	11											2379	−14	25
	12												27	31
	13													65



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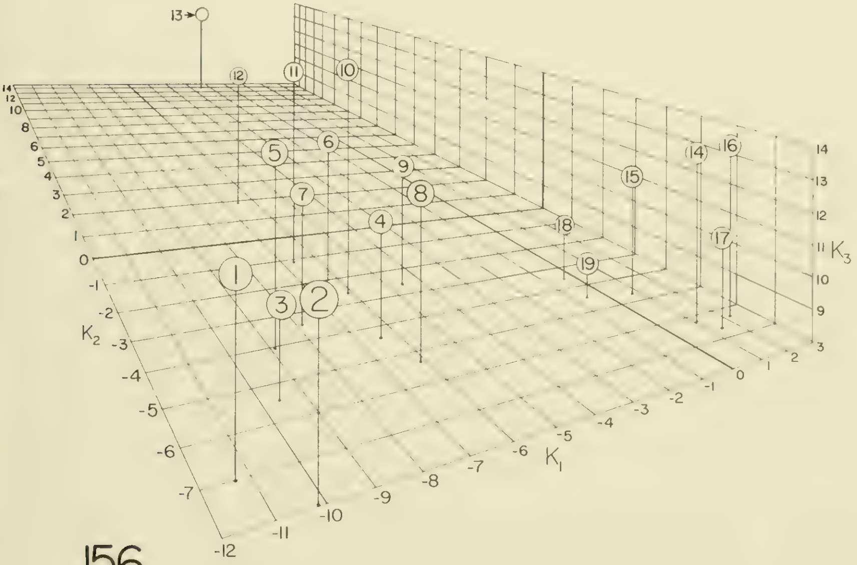

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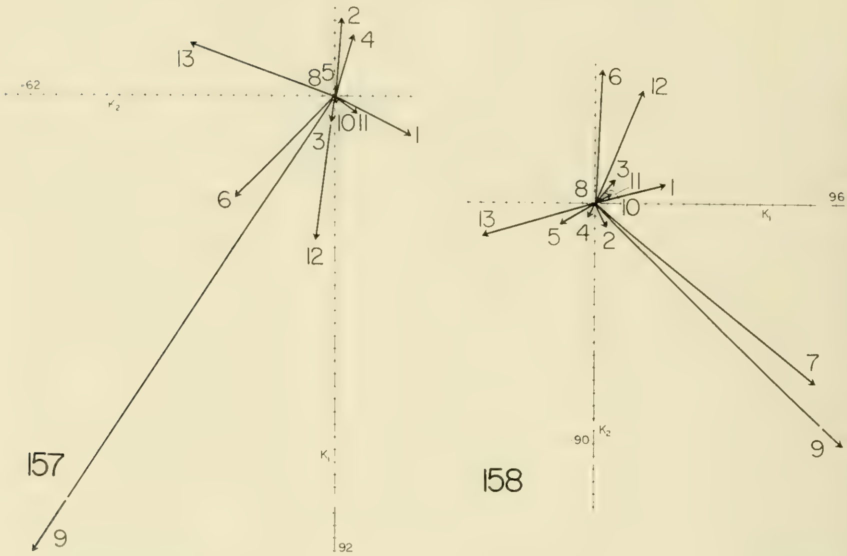
FIGS. 155-156. Distributions of the means of the 19 localities for males (Fig. 155) and females (Fig. 156) of *C. togata* in the first three discriminant functions (K_1, K_2, K_3), drawn as three-dimensional models, with numbered balls representing the means and vertical supports arising from the K_1, K_2 surface. Different sized balls indicate different distances from the viewer. The models are viewed from opposite directions, relative to the clusters.



FIGS. 157-158. Vectors for the 12 characters of males (Fig. 157) and 13 of females (Fig. 158) of *C. togata* for the first two discriminant functions. Each vector shows the change in the discriminant function that the corresponding character would produce if it varied independently. Units are same as in Figs. 155-156.

of the female elytral spine is small in all northwestern samples and great in southeastern samples.

The pattern of variation is complicated by specimens not measured from localities in west-central Texas. Three out of four specimens before me from Sand, Dawson County, Texas, are small and with completely white elytra (like specimens from locality 13 in Hudspeth County, Texas); the fourth is larger and similar to specimens from east-central New Mexico or southwestern Oklahoma. Of six specimens from Potash Lake, Gaines County, Texas, one has very wide markings, with only a narrow sutural band of the elytra not white; the others are more "normal."

Another characteristic of many southwestern populations of this species is the occurrence of occasional individuals with elytral basal dots (Fig. 91). Sometimes the dots are quite large and connect to the marginal maculation, but usually they are poorly developed and isolated. This has been noted in most samples from New Mexico, western Texas, and southwestern Oklahoma; and it even occurs as far northeast as southwestern Kansas and El Dorado, in east-central Kansas.

A clear division of the localities into two groups is shown in the above analysis, a coastal and eastern Texas form, *C. t. togata*, best characterized by the great retraction of the female elytral spine; and the northwestern populations, in which this spine is only slightly retracted. Within the latter group,

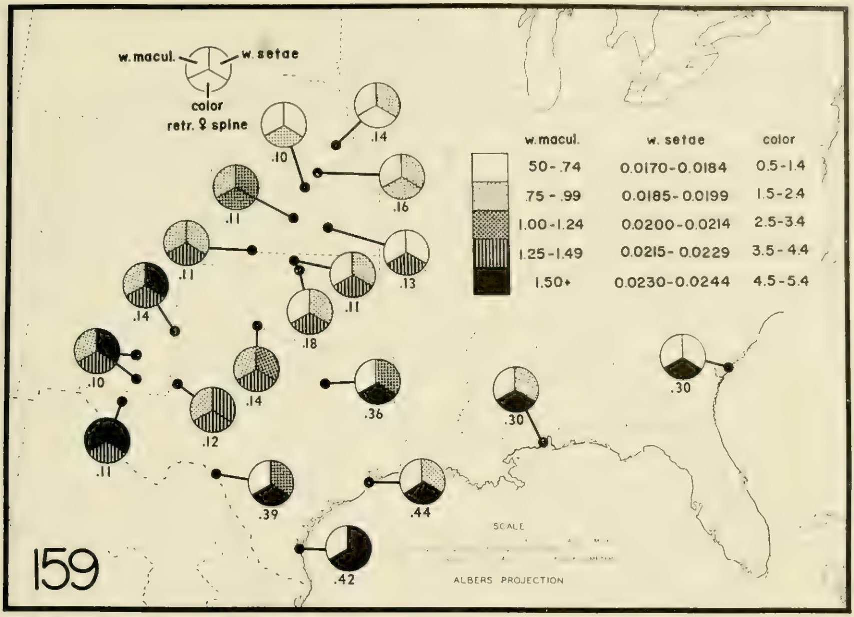

w. macul.
w. setae
color
retr. ♀ spine
.14
.10
.16
.11
.11
.13
.14
.11
.18
.10
.14
.36
.30
.30
.12
.11
.39
.44
.42
w. macul. w. setae color
50-.74 0.0170-0.0184 0.5-1.4
.75-.99 0.0185-0.0199 1.5-2.4
1.00-1.24 0.0200-0.0214 2.5-3.4
1.25-1.49 0.0215-0.0229 3.5-4.4
1.50+ 0.0230-0.0244 4.5-5.4
SCALE
ALBERS PROJECTION
159

FIG. 159. Geographic variation of four characters of *C. togata*: width of the maculation, width of pronotal setae, color, and retraction of the elytral spine of the female. Values for the first three characters have been pooled for the sexes and represented by different degrees of shading (upper right). Values for the fourth character are beneath each circle. The positions of the characters in the circles are shown at upper left.

a gradual cline exists in most characters measured, running from northeast to southwest, with no clear breaks or steps (or at least none in which there is any sort of character concordance). The type localities of the two valid named forms in this group are Clark County, Kansas, and Santa Rosa, New Mexico. Specimens from these areas are more similar to one another than are those from northern Kansas and Clark County or those from western Texas and Santa Rosa. Thus, only the earlier of these two names, *C. t. globicollis*, should be used. The form with completely white elytra from Hudspeth County, Texas, is certainly distinct enough to be called a subspecies, but as noted above, some specimens from west-central Texas are identical to or closely approach it; and intervening populations are more nearly "normal." Therefore, it does not seem advisable to recognize more than two subspecies within this species (Fig. 152). The two (female) specimens that I have seen from Pecos, Reeves County, Texas, appear to be intermediate between the two subspecies. One has a greatly retracted elytral spine and is greenish. The other has a slightly retracted spine and is cupreous. The maculation is fairly wide in both specimens.

C. togata probably evolved within its present range. It has no close relatives, so it is difficult to say whether it was first a coastal or an inland species. It eventually became widespread, evidently, in both coastal and inland habitats in the southern United States. Differentiation into races probably began in the form of a cline along the Rio Grande valley. The drier climates of late Tertiary or interglacial Pleistocene times no doubt exterminated many of the intermediate populations of the cline, resulting in evolution into the modern coastal and inland subspecies. Dispersal of the inland form to the northeast probably occurred during the Pleistocene. It could not have reached the Lincoln, Nebraska, area until after the Nebraskan glaciation.

The pattern of maculation and color variation seem clearly to be a result of selection to match the substrate color. In the drier Southwest, where saline habitats are more often covered by a white crust of salt, the width of the maculation is greatest. Populations with color values around 4 (cupreous) are found in the area with red soil (Figs. 159 and 108). Dark soils are prevalent in most other areas, and the beetles there are also dark. In some southwestern habitats, however, the soil is light gray, nearly white. Here, the elytra of *C. togata* are completely white or nearly so. The presence of the basal dot seems to be evolving in southwestern populations; it has the effect of increasing the amount of white on the elytra. Increased width of body setae also has the effect of making the beetle appear more white, a trend that has been noted in southwestern populations.

C. willistoni

This is a western species, most common in the Great Basin and Mojave Desert, and reaching its eastern limit in Kansas and Oklahoma (Fig. 160). Its distribution by county or state is the following:

KANSAS: Stafford; OKLAHOMA: Alfalfa, Beckham, Woods; TEXAS: Andrews; NEW MEXICO: Roosevelt, Torrance, Valencia; WYOMING: Albany, Carbon, Uinta; UTAH: Beaver, Box Elder, Cache, Davis, Emery-Rand County line, Iron, Juab, Millard, Salt Lake, Tooele, Utah, Washington; ARIZONA; NEVADA: Churchill, Lyon, Nye, Storey, Washoe; CALIFORNIA: Alameda, Inyo, Kern, Lassen, Los Angeles, Orange, Plumas, San Bernardino; OREGON: Harney, Lake. Town that could not be located: Farr Post (=Farrwest, Weber County ?), Utah. *Doubtful localities:* Kellwood, Manitoba; Colorado Springs, El Paso County, Colorado. The Los Angeles County (Seal Beach), Alameda Co. and Orange Co. (Irvine), California, localities (listed above) are somewhat questionable.

The following forms have been described within this species:

Cicindela willistoni Leconte, 1879. Type locality: Lake Como, Wyoming Territory.
Cicindela echo Casey, 1897. Type locality: Great Salt Lake, Utah.
Cicindela pseudosenilis W. Horn, 1900. Type locality: Owens Lake, Inyo County, California.
Cicindela echo amedeensis (emendation of *C. e. amadeensis* Casey, 1909). Type locality: Amedee, California. This form is clearly named for the type locality, but in the original description, the name is apparently misspelled.
Cicindela spaldingi Casey, 1924. Type locality: Callao, Utah.
Cicindela willistoni amargosae Dahl, 1939. Type locality: 4 miles north of Furnace Creek, Inyo County, California. This form is now recognized as a separate species.

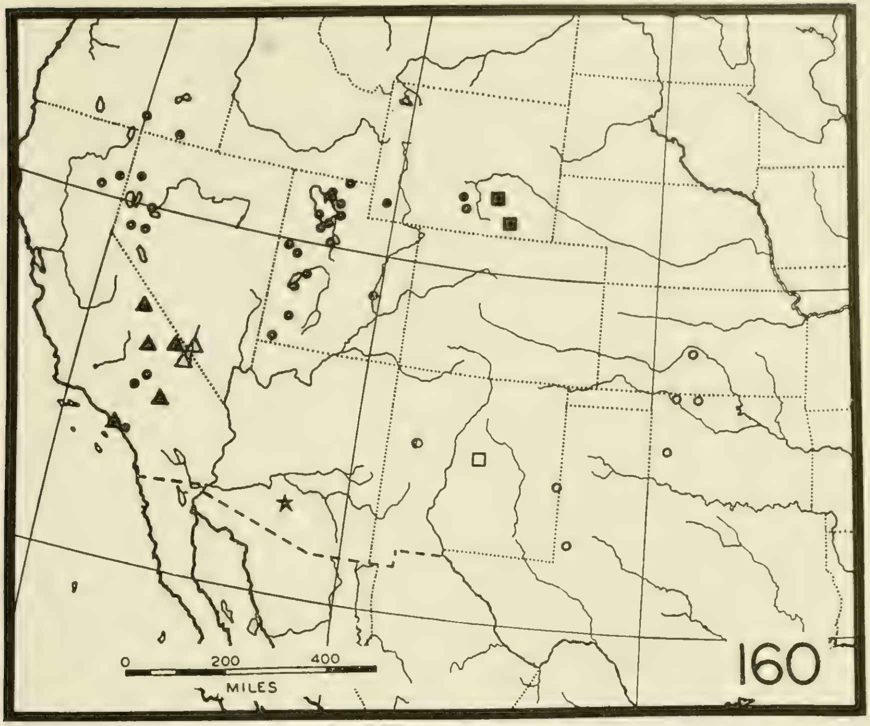


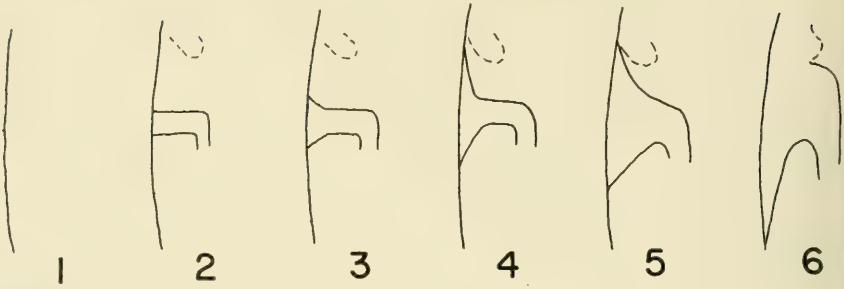
Fig. 160. Known distribution of *C. willistoni*. Shaded square=*C. w. willistoni*, shaded circle=*C. w. echo*, shaded triangle=*C. w. pseudosenilis*, open triangle=*C. w. praedicta*, open square=*C. w. estancia*, open circle=*C. w. hirtifrons*, half shaded circle=population of uncertain status, star=state record.

Cicindela willistoni praedicta Rumpp, 1956. Type locality: 3.5 miles south of Shoshone, Inyo County, California.

Cicindela willistoni estancia Rumpp, 1961. Type locality: 7 miles east of Willard, Torrance County, New Mexico.

In recent years, five subspecies have been recognized: *C. w. willistoni*, the reddish brown form with marginally expanded markings; *C. w. echo*, the brownish form with usually "average" markings; *C. w. pseudosenilis*, the blue or blue-green form, sometimes with expanded markings; *C. w. praedicta*, the small blue or blue-green form with reduced markings or none at all; and *C. w. estancia*, the feddish brown form with markings so expanded, the elytra are nearly completely white.

In the study of geographic variation, the following characters were measured: (1) length of left elytron; (2) width of left elytron; (3) width of labrum; (4) length of labrum, including tooth; (5) shape of base of middle band in arbitrary units (Fig. 161); (6) smallest width of transverse portion of middle band (Fig. 162); (7) number of setae on vertex and frons, except



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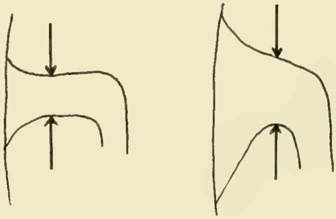

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FIGS. 161-162. Illustrations of certain characters measured on elytra of *C. willistoni*; FIG. 161, arbitrary units for shape of base of middle band; FIG. 162, smallest width of transverse portion of middle band.

the several supraorbital sensory setae near the medial margins of the eyes; (8) color, using color wheel.

Specimens from seven localities were measured. The localities and sample sizes are given in Table 44. Sample sizes are adequate except for females from Oregon (specimens from Oregon were lumped into one sample) and Kern County, California. Unfortunately, these seven localities do not encompass all the recognized forms mentioned above; no specimens of *C. w. estancia* were available.

The means for the characters and localities are given in Tables 45 and 46. Analyses of variance of the individual characters showed that there are significant differences ($p < 0.01$) among the means of all characters in males and all characters in females except number 1, which is significant at the 5% level. Pooled within-locality variance-covariance matrices are given in Tables 47 and 48. The sums of the among-locality variance components are 218.88 for males and 429.67 for females. The first four components for males and the first three for females are highly significant ($p < 0.01$), and the fourth component for females is significant at the 5% level. The first three functions account for 96.66% of the variance (among localities relative to that within)

TABLE 44. Localities and sample sizes of the specimens of *C. willistoni* measured.

Locality	N ♂	N ♀
1. KANSAS, Stafford Co., 11 mi. n.e. of Hudson	12	12
2. WYOMING, Carbon Co., Como Lake	12	12
3. UTAH, Salt Lake Co., vicinity of Salt Lake City and Saltair	12	12
4. OREGON, Lake Co., Rest Lake, Summer Lake; Harney Co., Alvord Hot Springs	8	3
5. CALIFORNIA, Inyo Co., Olancho (Owens L.)	12	12
6. CALIFORNIA, Kern Co., Saltdale	12	4
7. CALIFORNIA, Inyo Co., 3.5 mi. s. of Shoshone	12	12

TABLE 45. Means of seven localities (see Table 44) and seven characters for males of *C. willistoni*. Values for characters 1-4 are in mm.

Locality	Character 1	2	3	4	5	6	7
1	7.61	2.31	1.82	0.93	3.98	0.59	31.0
2	7.66	2.39	1.82	0.94	6.09	1.38	22.2
3	7.51	2.31	1.74	0.81	4.18	0.80	5.7
4	7.96	2.39	1.87	0.88	3.75	0.85	5.6
5	7.69	2.30	1.82	0.88	3.50	0.86	6.2
6	7.63	2.33	1.81	0.88	4.79	1.15	4.8
7	7.96	2.03	1.63	0.79	1.37	0.15	5.2

TABLE 46. Means of seven localities (see Table 44) and seven characters for females of *C. willistoni*. Values for characters 1-4 are in mm.

Locality	Character 1	2	3	4	5	6	7
1	7.84	2.59	1.84	0.96	4.01	0.56	38.3
2	7.84	2.64	1.85	1.00	5.99	1.28	28.6
3	7.64	2.53	1.81	0.86	3.54	0.79	6.8
4	7.58	2.46	1.80	0.89	3.63	0.74	6.3
5	7.80	2.50	1.85	0.91	2.88	0.77	5.8
6	7.82	2.56	1.87	0.92	4.98	1.23	5.3
7	7.33	2.26	1.70	0.85	1.00	0.00	5.8

in males and 98.80% in females. The distributions of the means in the first three discriminant functions are shown in Figures 163 and 164. Localities 3-6 form a loose cluster (especially in males), while the others are widely scattered.

The results of the simultaneous testing procedure show that all combinations of pairs of means are significantly different at the 5% level except 4 vs. 5 for males and 3 vs. 4 for females.

TABLE 47. Pooled within-locality variance-covariance matrix for males of *C. willistoni.* Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "1082"=0.1082.

					Character			
		1	2	3	4	5	6	7
Character	1	1082	286	246	148	540	224	1582
	2		106	72	43	205	80	391
	3			69	40	113	63	427
	4				31	90	36	103
	5					2521	580	—474
	6						341	—508
	7							184355

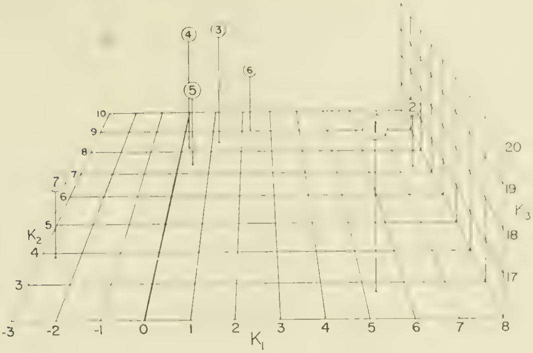
TABLE 48. Pooled within-locality variance-covariance matrix for females of *C. willistoni.* Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "1748"=0.1748.

					Character			
		1	2	3	4	5	6	7
Character	1	1748	569	394	268	208	189	—2314
	2		235	136	93	45	58	—523
	3			105	67	64	41	—462
	4				50	39	28	—361
	5					1060	219	1186
	6						183	—681
	7							193125

Sets of vectors (Figs. 165 and 166), plotted for the first two functions, show geographic trends of the seven characters when compared with Figures 163 and 164. Specimens with high values in K_2 and low values in K_1 (localities 1 and 2) have a long, narrow labrum, while specimens from other localities have wider labra. Specimens low in K_1 and K_2 (locality 7) have long elytra and narrow markings, while specimens high in K_2 (localities 3-6) have wide elytra and broad markings.

The results of the color analysis are shown in Figure 167. Samples from Oregon and Utah consist mostly of dark purplish to dark red-green (appears brown-green) individuals. The southwesternmost sample in California is similar but contains many green individuals. The other two California samples contain mostly blue to blue-green individuals. The samples from Wyoming and Kansas contain many individuals with brighter colors, ranging from purplish to reddish to red-green (and green in Wyoming).

These analyses confirm the existence of four of the above five recognized subspecies (the fifth, *C. w. estancia*, is clearly distinct because of its extremely wide markings). Localities 2 *(C. w. willistoni)* and 7 *(C. w. praedicta)* are



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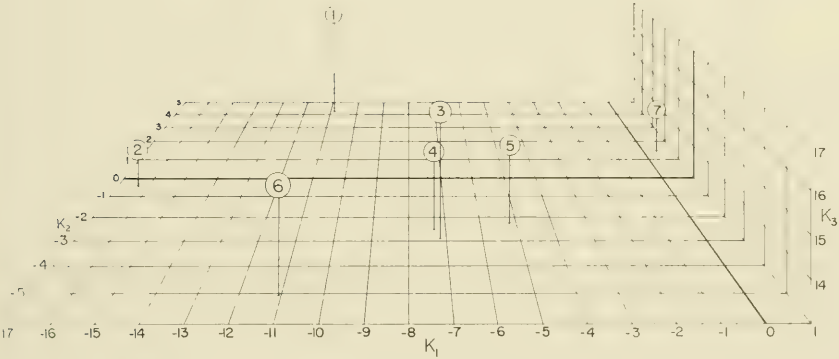

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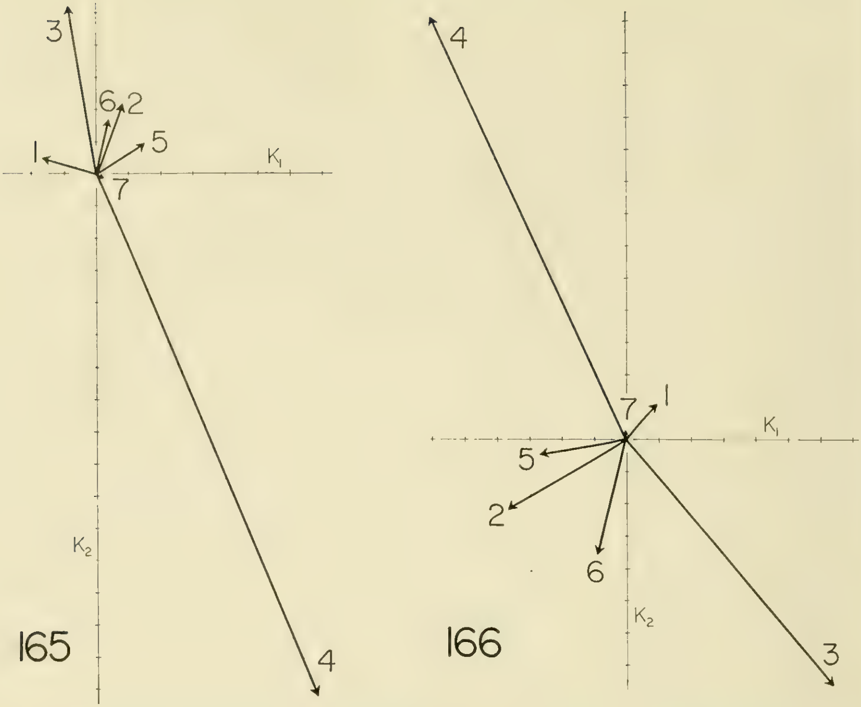
FIGS. 163-164. Distributions of the means of the seven localities for males (Fig. 163) and females (Fig. 164) of *C. willistoni* in the first three discriminant functions (K_1, K_2, K_3), drawn as three-dimensional models, with numbered balls representing the means and vertical supports arising from the K_1, K_2 surface. Different sized balls indicate different distances from the viewer. The models are viewed from opposite directions, relative to the clusters.

widely separate from all other in the statistical analysis. Locality 5 *(C. w. pseudosenilis)* is quite similar to localities 3, 4, and 6 *(C. w. echo)* except in color. Specimens from Kern County, California (locality 6, Saltdale, also Mojave) differ from other populations of *C. w. echo* in having the middle band nearly always very wide in the transverse portion, sometimes broadly confluent with the humeral lunule. In other populations of *C. w. echo*, only occasional individuals exhibit this tendency. Also many (about 17%) of the Kern County specimens are dark green or blue-green. On the basis of these characters and their geographical isolation, they could probably be separated as a subspecies, although this will not be done at present. The Kansas sample



FIGS. 165-166. Vectors for the seven characters of males (Fig. 165) and females (Fig. 166) of *C. willistoni* for the first two discriminant functions. Each vector shows the change in the discriminant function that the corresponding character would produce if it varied independently. Units are same as in Figs. 163-164.

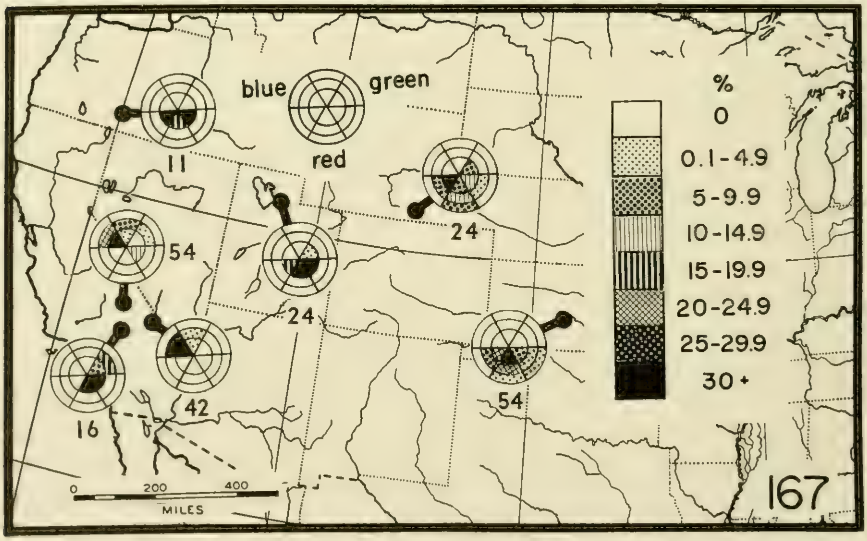

blue
green
red
11
54
24
24
42
16
54
%
0
0.1-4.9
5-9.9
10-14.9
15-19.9
20-24.9
25-29.9
30+
0
200
400
MILES
167

FIG. 167. Result of color analysis of *C. willistoni*, using the color wheel. Different degrees of shading indicate different percentages of the sample. The positions of the three major colors are shown at top center. Numbers show the sample size for each locality.

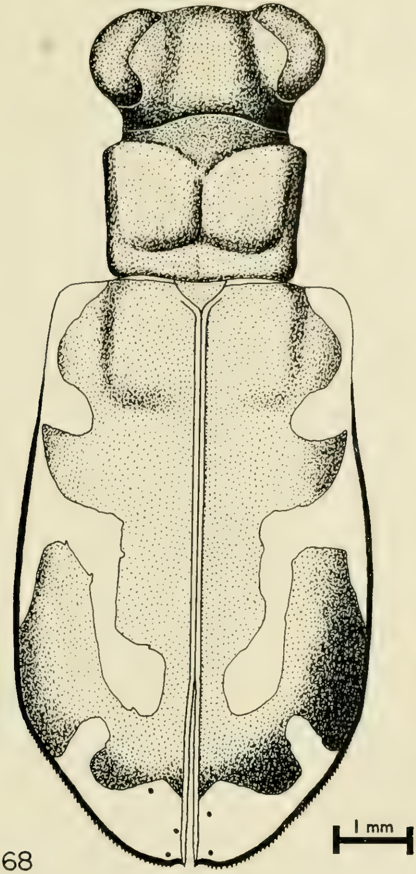


Fig. 168. *Cicindela willistoni hirtifrons,* new subspecies; dorsal aspect of male (setae omitted).

was widely separated from the others by the statistical analysis; it represents what seems to be a clearly defined new subspecies, described below:

Cicindela willistoni hirtifrons, new subspecies (Fig. 168)

Head: Labrum with single median tooth, length usually more than half the width; antennal scape with 10-25 stout erect setae; clypeus and genae glabrous; frons and vertex with 16-51 fine erect setae medially, some long, some short (not including several pairs of sensory setae near medial margins of eyes); *Thorax:* pronotum glabrous medially, with long, erect to partly decumbent setae laterally; proepisternum, proepimeron, procoxae, mesepimeron, mesocoxae, metaepisternum, and lateral parts of metaepisternum and metacoxae with dense, long to medium erect setae; mesepisternum with a few erect setae; mesosternum and medial portions of metasternum and metacoxae with sparse short setae; prosternum glabrous; lateral margins of pronotum subparallel, diverging slightly anteriorly; *Abdomen:* venter with dense to sparse decumbent to erect setae; *Elytra:* male, gradually widened to one-half to two-thirds their length, then gradually narrowed to apical fifth, then abruptly narrow to rounded apex; female, margins much expanded at middle from basal fourth to apical third, then rounded to apex; posterior margin microserrulate; spine apical to slightly retracted; markings similar to those of typical *C. w. echo*, but middle band often narrower; humeral lunule and middle band usually connected by narrow marginal expansion of middle band; apical lunule and middle band not connected; surface shiny or greasy-appearing; *Color:* dorsum and front of head bronze or cupreous, with areas of green and blue; genae blue and green; lateral portions of thorax cupreous, green, and blue; venter green to purplish blue; pronotum bronze or cupreous with depressions green and blue; elytra between markings cupreous to purple-cupreous to bronze to greenish bronze, sometimes quite green when viewed from an oblique angle.

Type locality: Big Salt Marsh, 11 mi. N.E. of Hudson, Stafford Co., Kansas. Holotype male, allotype female, and 15 paratopotypes (11 males, four females), 7 April 1965 (Harold L. Willis) in the Snow Entomological Museum, University of Kansas. Ninety-eight paratopotypes, 9 April 1964, 7 April 1965, 21 June 1965 (Harold L. Willis): ten in the U.S. National Museum; ten in the American Museum of Natural History; 15 in the collection of N. L. Rumpp; five in the collection of G. C. Gaumer; four in the collection of J. Stamatov, Armonk, New York; three each in the collections of R. Freitag, R. C. Graves, R. L. Huber, and J. K. Lawton; two in the collection of J. F. Payne, and the rest in the author's collection. Eight paratopotypes, 23 May 1965 (Paul E. Slabaugh), in the collection of P. E. Slabaugh.

Fourteen paratypes: OKLAHOMA, 2.5 mi. S.W. of Plainview, Woods Co., 3 May 1964, 3 June 1963, 8 June 1965, five specimens in the author's collection; 3 mi. E. of Cherokee, Alfalfa Co., 11 April 1931, 4 June 1963, 7 June 1931, 11 June 1931, 15 June 1935, eight specimens, five in the University of Oklahoma, one in the U.S. National Museum, one in the Museum of Comparative Zoology, Harvard University, and one in the author's collection; NEW MEXICO, 4 mi. E., 1 S. of Arch, Roosevelt Co., 9 June 1965, one specimen in the author's collection.

Distribution: Central Kansas, western Oklahoma, west-central Texas, east-central New Mexico, and possibly west-central New Mexico (Fig. 160).

Diagnosis: Differs from *C. w. willistoni* and *C. w. estancia* in narrower markings, with the humeral lunule and middle band separate or narrowly connected, not broadly confluent; from all other subspecies by the large number of medial setae on the frons and vertex (more than 15, rather than

10 or fewer), the relatively longer labrum (width/length ratio usually less than 2.0, rather than more than 2.0), and the generally reddish brown dorsal color, rather than (usually) dark brown, greenish, or blue. This subspecies shares the very setose head, longer labrum, and reddish dorsal color with *C. w. willistoni* and *C. w. estancia.*

Four out of 24 or 16.7% of specimens of *C. w. hirtifrons* have a labral width/length ratio of 2.0 or greater. Out of 99 specimens representing *C. w. echo*, *C. w. pseudosenilis*, and *C. w. praedicta*, 17 or 17.2% have a labral width/length ratio of less than 2.0; however, these values range from 8.4% for *C. w. echo* to 29.1% for *C. w. praedicta.*

The one specimen from Roosevelt County, New Mexico, has quite wide markings, the apical lunule and middle bands nearly being connected at the margin. The Andrews County, Texas, record is based on a second instar larva. About half the specimens from Oklahoma have slightly wider markings than most Kansas specimens. The record from Beckham County, Oklahoma, is based on Ortenburger and Bird (1933); no specimens have been examined from there. Only about 3% of the Kansas specimens have so much green on the dorsum that they appear green-brown; however, it is a brighter green than occurs in western subspecies. About 4% of the Kansas specimens are a dark brown and might be confused with *C. w. echo*, but the number of head setae easily separates them. All the Oklahoma specimens and the New Mexico specimen are cupreous-brown, with no indication of green. Occasional individuals of *C. w. echo* are reddish brown or reddish green; however, as mentioned, the number of setae on the frons and vertex completely separates the two forms (if the head setae have been rubbed off, one can find what their approximate number was by counting the punctures from which they arose). The exact status of the population at Grants, Valencia County, New Mexico, is not known. No specimens were available for study; however, N. L. Rumpp *(in litt.)* said that they are similar to the Kansas specimens.

I do not know the subspecies of the population in Arizona (Fig. 160) because I have seen no specimens from there. Two specimens reputedly from Orange County, California, that are dark blackish and have fairly wide markings are being called *C. w. echo* for the present. One specimen labelled Alameda County and two from Los Angeles County, California, are typical *C. w. pseudosenilis.*

Wickham (1904a, b) thought that *C. w. echo* arose within the Great Basin, that *C. w. pseudosenilis* has been isolated at Owens Lake, California, since at least early Pleistocene, and that *C. w. willistoni* was separated from the other forms of the species (known to him at that time) by the rising mountains of late Tertiary. Rumpp (1961) postulated that *C. willistoni* arose from an ancestor that lived in northern North America in the warm Cretaceous. As climates cooled during the Tertiary, the ancestral species moved south and became widespread from Colorado to the Pacific coast, gradually assuming the character of *C. willistoni*. He stated that after its formation, *C. willistoni* evolved only slightly, coming through the Miocene "in its present form." The rising mountains of the Cascadian Revolution isolated populations in the Great Basin, Wyoming, and New Mexico. The various subspecies began evolving during the Pliocene or earlier.

Wickham's and Rumpp's theories on the evolution of *C. willistoni* seem quite plausible, although it is hard to imagine that little or no evolution has occurred since the Miocene. The selective forces that acted to produce the different geographic races (matching the color of the substrate seems to be an important one, climatic conditions are another) would seem to be still operating. Wickham and Rumpp did not know of the occurrence of *C. willistoni* in the central United States, and neither mentioned that populations from east of the Rocky Mountains have quite setose heads, while those in the West are sparsely setose (Wickham noted a difference, but only in passing). The closest relatives of *C. willistoni* (it has no extremely close relatives) are *C. senilis* and the *C. tranquebarica* complex, all of which have very setose heads. Thus, I conclude that the primitive condition in *C. willistoni* is a densely setose head, and that the western forms are losing this character. The markings of the ancestral species were probably much like those of *C. w. echo* or *C. w. hirtifrons*, from which expansions or reductions evolved. The primitive color was most likely brownish; populations of *C. w. pseudosenilis* still contain occasional brown or half brown individuals, hinting of its origin from a *C. w. echo*-like ancestor. During the late Tertiary, *C. w. echo* must have been distributed nearly throughout the Great Basin; in fact, it transgressed into eastern Utah and southwestern and south-central Wyoming, leaving relict populations (Fig. 160). During dry interglacials, many populations were no doubt exterminated, leaving large gaps in the range of *C. w. echo*, particularly in eastern Nevada. *C. w. hirtifrons* and *C. w. estancia* probably evolved from a common ancestor (the same one that left populations in Wyoming which became *C. w. willistoni*) that moved south into New Mexico in the Tertiary and then dispersed northeastward through Texas and Oklahoma into Kansas. A population was "trapped" in the Estancia Valley of central New Mexico and became the very widely maculate *C. w. estancia*, while *C. w. hirtifrons* retained a "normal" maculation. The soil in the habitat of the former is tan and sandy, and is usually covered by a white alkaline crust. In the range of *C. w. hirtifrons*, soils are usually red clay or sand, and the climate is moister (especially in the eastern part). Thus, these forms have apparently evolved toward a better match of their substrate.

GENERAL PATTERNS

The seven species discussed exhibit certain general patterns within the central United States. The most striking are the increase in red color (in all but *C. fulgida*) in the region of red soils, and the increase of white maculation in the drier western regions, both of which have been discussed repeatedly above. Another is the distinctness of the populations in the Lincoln, Nebraska, vicinity. Four of the species have more or less distinct forms occurring there: the small, always reddish form of *C. circumpicta*, the black form of *C. fulgida*, the narrowly maculate *C. nevadica lincolniana*, and a form of *C. togata* in which the edges of the white maculation are brownish and indistinct (occasional specimens from northern Kansas show this also). As mentioned earlier, I think this means that these populations survived the last one or two Pleistocene glaciations at this locality, while other populations of their species were driven south or exterminated.

FAUNAL RELATIONSHIPS

The 13 species in this study are divisible into two groups, reflecting their principal distribution and phylogeny: 1) the northern species; these are the more primitive species that are adapted to cooler climates (most active in the spring and fall in the central United States), and that have primarily northern distributions; 2) the southern species; these include the more advanced species that are adapted to warm climates (active in the summer in the central United States), and that have primarily southern distributions. The northern species are *C. duodecimguttata*, *C. fulgida*, *C. hirticollis*, *C. repanda*, *C. tranquebarica*, and *C. willistoni*. The southern species are *C. circumpicta*, *C. cuprascens*, *C. macra*, *C. nevadica*, *C. punctulata*, *C. schauppi*, and *C. togata*. The probable evolutionary relationships of these species were discussed in the section on phylogeny.

SUMMARY

1. Aspects of the bionomics and zoogeography of 13 species of *Cicindela* (Coleoptera: Cicindelidae) living in saline habitats of the central United States (southern Nebraska, western Missouri, Kansas, and Oklahoma) were studied.

2. A review was made of the published works concerning the bionomics of *Cicindela*. By watching beetles in the field and rearing them in the laboratory, new knowledge was obtained on such subjects as oocyte development, gross embryology, length of stadia, pupal development, post-emergence changes of the adult, feeding of larvae and adults, mating behavior, oviposition, and ecological relationships. The larvae of four species were described

for the first time *(C. fulgida, C. nevadica, C. togata,* and *C. willistoni)* and one was redescribed *(C. circumpicta).* The species show a tendency to avoid competition by inhabiting different microhabitats and by being active at different times of the year; however, there is much overlap. Adaptations for living in saline habitats were noted; most are possessed by species not inhabiting such areas, and many of the species in this study are more common in nonsaline habitats.

3. The zoogeography of seven species was studied for their entire ranges *(C. circumpicta, C. cuprascens, C. fulgida, C. macra, C. nevadica, C. togata,* and *C. willistoni*). Geographic variation of morphological characters was studied using generalized discriminant functions. The results were used to help confirm or reject the existence of subspecies. The subspecies *C. circumpicta salinae* and *C. togata fascinans* were rejected. One new subspecies, *C. willistoni hirtifrons,* was described.

4. Using the patterns of geographic variation and evidence from past geological history, hypothetical schemes of evolution and dispersal were proposed. An important selecting pressure acting on all species but *C. fulgida* seems to be increasing the resemblance of the dorsum of the adult to the color of the substrate. In regions having red soil, populations of beetles show a pronounced tendency toward reddish colors. In the drier western parts of their ranges, many species have an increased amount of white on the body, particularly the white elytral markings. This seems to result from the fact that in these areas, saline habitats are more often covered by a crust of white crystalline salts; in moister areas, the salts are more often dissolved and the color of the soil is apparent.

5. It is suggested that the Lincoln, Nebraska, vicinity was a refuge for at least five species during the late Pleistocene glaciations.

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THE UNIVERSITY OF KANSAS
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INTERACTION OF THE BULL'S-HORN ACACIA (*ACACIA CORNIGERA* L.) WITH AN ANT INHABITANT (*PSEUDOMYRMEX FERRUGINEA* F. SMITH) IN EASTERN MEXICO

By

Daniel H. Janzen

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Interaction of the Bull's-Horn Acacia (*Acacia cornigera* L.) with an Ant Inhabitant (*Pseudomyrmex ferruginea* F. Smith) in Eastern Mexico[1]

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ABSTRACT

The interaction between a swollen-thorn acacia, *Acacia cornigera,* and an ant inhabitant, *Pseudomyrmex ferruginea,* is described from the lowland coastal plain in eastern Mexico. A detailed study of the bionomics of the acacia and the ant is presented to aid in the interpretation of experiments with the interaction. The experimentation lasted a year (Sept. 1963 to Aug. 1964), and was conducted in the second growth vegetation in pastures, roadsides, and fallow corn fields in the area between Temascal, state of Oaxaca, and La Granja, state of Veracruz. Additional observations of the acacia and the ant in other parts of their range north of Coatzacoalcos, Veracruz, showed that the populations in the Temascal-La Granja area are representative of those in eastern Mexico.

The bull's-horn acacia, *A. cornigera,* is a representative swollen-thorn acacia with well-developed foliar nectaries, enlarged stipular thorns, and small nutritive organs (Beltian bodies) borne at the tip of each leaf segment. The colony of *P. ferruginea* living in the enlarged stipules obtains sugars from the foliar nectaries, and oils and proteins by eating the Beltian bodies.

A. cornigera is a woody plant with an extremely high growth rate. It is intolerant of shading and is a member of the canopy, or is emergent, during the first 6-12 years of regeneration. While its original habitat was natural disturbance sites (river banks, arroyos), it has invaded with great success the man-made disturbance sites that are not burned on an annual basis; nearly all of its regeneration in such sites is as suckers from old root stocks and requires that the ant colony move from the cut acacia into the new suckers. When the acacia is not occupied

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for natural causes, or has its ants removed experimentally, it is subject to severe damage by phytophagous insects; these are insects which normally feed on other species of plants.

Morphologically, *P. ferruginea* is a representative pseudomyrmecine ant; behaviorally it has a number of outstanding characteristics associated with its interaction with swollen-thorn acacias. The workers patrol and clean the surfaces of the acacia, and bite and sting animals of all sizes that contact the plant. The workers maul any other species of plant that contact the acacia and in many cases, any that grow under the acacia. The colony attains a very large size and up to 25 per cent of the workers may be active on the surface of the acacia both day and night. The larger the colony becomes, the smaller is the damage sustained by the plant from defoliators. The colony enhances its own probability of survival by protecting the acacia on which it is completely dependent for food and domatia.

In the course of the study, 50 control or treatment subplots were established. The ants were removed from the acacias by spraying with parathion, clipping the thorns, or cutting and removing the occupied shoot. Measurements throughout the year of the height increment, condition, freedom from vines, leaf and thorn production, and biomass production, showed that all of these parameters are greatly reduced if the ants are removed from the acacia. In the experimental plots, this was almost entirely due to phytophagous insect damage, and subsequent shading of the stunted shoots. Based on these data, and observations of naturally unoccupied acacias, it is concluded that a shoot of *A. cornigera* must be occupied by a colony of *P. ferruginea* for a substantial part of its life to produce seeds and become a part of the reproductive population. The ant is dependent upon the acacia for survival and the acacia is dependent upon the ant for normal population development; the interaction between the two can therefore be properly termed one of obligatory mutualism.

INTRODUCTION

Within the mimosaceous plant genus *Acacia*, at least nine neotropical species have an obligate or consistent relationship with ants. These are often called "ant-acacias." In all the known obligate relationships, the ants belong to the genus *Pseudomyrmex* (in most previous literature cited as *Pseudomyrma*), and at least five species are involved. They are often called "acacia-ants" and live in the swollen stipular thorns which are characteristic of ant-acacias. They feed almost entirely on the nectar and nutritive bodies (Beltian bodies) produced by the acacia. Most acacia-ants have been recorded only from living ant-acacias and there is little doubt that they are dependent on the acacia for existence. However, the question of whether or not the ant-acacia is benefited by the presence of the acacia-ant has been outstanding in the literature dealing with ants and plants since Belt's (1874) often-quoted description of the relationship of *Pseudomyrmex belti* Emery with *Acacia costaricensis* Schenck in Nicaragua (Wheeler, 1942). The study described in the present paper is an attempt to resolve this question. The species pair *Pseudomyrmex ferruginea* F. Smith and *Acacia cornigera* L. was chosen for intensive study. In previous literature, *P. ferruginea* is discussed as *Pseudo-*

myrmex belti fulvescens Emery or *Pseudomyrmex fulvescens* Emery (Janzen, 1967a).

The aggressive behavior of many species of acacia-ants toward humans coming in contact with the acacia has led to numerous published opinions that the ants "protect" the plant from phytophagous animals (Belt, 1874; Delpino, 1886-1889; C. Darwin, 1877; F. Darwin, 1877; Schimper, 1888; Wasmann, 1915, 1916; Schwarz, 1917; Safford, 1922; Standley, 1928; Alfaro, 1935; and Brown, 1960). However, others have considered that the thorns themselves are sufficient protection against browsing mammals, and that the acacia-ants have little impact on the action of phytophagous arthropods (Rettig, 1904; Ule, 1905, 1906; Wheeler, 1913, 1942; and Skwarra, 1930, 1934a, 1934b). With the exception of Brown's (1960) question-posing paper, this argument has not been treated in detail since Wheeler's (1942) and Uphoff's (1942) literature review. The portions of the populations of *A. cornigera* and *P. ferruginea* treated in this paper have received little specific attention in these discussions (except Skwarra's papers). It was apparently believed that all swollen-thorn acacias had approximately the same type of interaction with the species of *Pseudomyrmex* obligatorily associated with *Acacia*. As a consequence, little effort was made to understand each ant-acacia interaction as a separate system. A demonstrated or postulated point about the interaction of one species of acacia with one species of ant was usually regarded as applicable to all. Associated with this, there was little hesitation to propose hypotheses which were intended to encompass all swollen-thorn acacias, and at times, all plants with obligate ant associates. The data presently available indicate that the various interaction systems between ants and acacias cannot be discussed in general terms until more information has been gathered. The same must be said for other genera of plants and the ants associated with them.

The data in the literature dealing with swollen-thorn acacias that have been summarized by Wheeler (1942:94-116) do not merit further detailed discussion until the acacias and their ants have been further studied. However, there are a number of papers in which the authors arrived at a definite conclusion about the presence of a symbiotic relationship between the swollen-thorn acacias and their ant inhabitants.

Of those who supported the idea of a symbiotic relationship, Belt (1874) is the most often referred to. His feelings can be summed as "These ants form a most efficient standing army for the plant, which prevents not only the mammalia from browsing on the leaves, but delivers it from the attacks of a much more dangerous enemy—the leaf-cutting ants." He then restates this as "I think that these facts show that the ants are really kept by the acacia as a standing army, to protect its leaves from the attacks of herbivorous mammals and insects."

Brown (1960) feels that "On the face of it, Belt's opinion has long seemed to me more attractive than that of the exploitationists." The "exploitationists" are those such as Wheeler who felt that the ants were merely exploiting the acacia and that the acacia was not affected by their presence. Brown continues on to discuss the evidence available that supports the idea that the ants may protect the acacias from browsing mammals. He concluded with, "The claims of the protectionist school for the adaptive nature of some kinds of extrafloral nectaries and ant domiciles in attracting insect 'guards' against phytophagous insects also seem reasonable, but proper study of the problem has scarcely begun."

While never having seen the ants or the acacias in their natural habitat, F. Darwin (1877) has rather enlarged on Belt's discussion in saying, "The ants form a standing army for the tree, and not only prevent cattle etc. browsing on it, but also protect it from the ravages of the leaf-cutting ants. So serious is the latter danger, that the tree is actually unable to exist without its guard of colonists."

After observing the stands *of Acacia sphaerocephala* in the Tampico, Tamaulipas, Mexico area, Schwarz (1917) had the following comments. ". . . the writer can fully corroborate the original observations of Mr. Belt to the effect that the ants effectually defend the acacia trees against the attacks of man, cattle and insects. No leaf-eating caterpillers, no aphids, nor coccids are seen on the trees; no leaf-cutting ants ever defoliate the same."

After examining the ants and acacias in the field in Costa Rica, Alfaro (1935) came to the conclusion that the aggressive nature and well developed sting of the ants constituted the best defense of the plant against the small enemies that could attack it. He appears to agree with Belt's conclusion that the ants serve to keep leaf-cutter ants from defoliating the shoot.

Wasmann expressed the view both in 1915 and 1916 that we may still speak of a true symbiosis between the ant-acacias and the acacia-ants, rather than merely a case of parasitism by the ant. The reiteration of this view (1916) was in response to Wheeler's (1913) paper. Wasmann's feeling that a true symbiosis exists is accompanied by an exposition of a possible means of evolving such a symbiotic system.

While the above authors who believed that a symbiotic relationship existed were not referring explicitly to *A. cornigera* and *P. ferruginea* in the geographic area where the present study was conducted, this study has shown that their beliefs were in general correct in respect to this pair of species. The degree to which they are correct in respect to other species pairs must remain undecided since there is not sufficient data in the literature to discuss the question. The author is at present gathering data on these other species pairs.

Of those who supported the idea that the ants bear only an exploitationist relationship to the acacia, there were only two, Wheeler and Skwarra. In 1913, Wheeler (borrowing von Ihering's (1907) conclusion about plants in the genus *Cecropia* and their ants) stated, "I believe, therefore, that we may adopt von Ihering's point of view, and say that *Acacia cornigera, hindsii,* and *sphaerocephala* have no more need of their ants than dogs have of their fleas. If this is true, the relation between the ants and plants is not one of symbiosis, but one of parasitism." By 1942 Wheeler had not changed his mind. He stated that ". . . the 54 different organisms . . . listed above as associated with the bullhorn Acacias . . . are sufficient . . . to show, first, that these plants have plenty of natural enemies and are in this respect like other nonmyrmecophytic trees and shrubs in the tropics, and second, that the obligate ant tennants, though more virulent than those of *Cordia alliodora* and the *Cecropias,* are nearly or quite as tolerant of alien ants and other insects on the same plants. I therefore reiterate my statement of 1913 that the relations existing between the Acacias and the obligate Pseudomyrmas are not properly those of symbiosis, in which the plants have adapted themselves to the ants, but those of host and parasite, in which the adaptations are solely on the part of the ants."

After field observations in the state of Veracruz, Mexico, Skwarra (1934a) concluded that the acacia-ants are not capable of protecting the leaves, flowers and fruits of the shoots from destructive insects and that the ants are therefore not useful to the plant. Her observations were based entirely on *A. cornigera* and *A. sphaerocephala* and their various ant inhabitants. Her conclusions were primarily based on finding bird nests and several species of insects on occupied shoots. Skwarra's findings are not included in Wheeler's 1942 paper, but had they been, he undoubtedly would have used them to support his own opinion.

While a definitive statement cannot be made about the correctness of Wheeler's opinions in respect to other ant-acacias, the present study has shown that his opinion was incorrect in respect to *A. cornigera* and *P. ferruginea* in the study area. Skwarra's statements of facts about acacias and their ant inhabitants appear quite correct but her conclusions based on them have been refuted by the evidence gained in this study. The major problem of both workers was in failing to observe what happens to the acacia when it is not occupied by a colony of *P. ferruginea*; they were only concerned with what happens to the acacia when it is occupied.

Both *A. cornigera* and *P. ferruginea* range from northeastern Mexico to Guanacaste Prov., Costa Rica. The present study is concerned with the populations in the coastal lowland and bordering foothills of the area from Coatzacoalcos, in the state of Veracruz, Mexico, northwest to the northern range limits around Tampico and Cd. Mante, in the state of Tamaulipas (henceforth designated "study area"). The other acacias with swollen thorns and the *Pseudomyrmex* that occasionally are found in them in the study areas are discussed for comparative purposes (*Acacia chiapensis* Safford and *Acacia sphaerocephala* Schl. and Cham.; *Pseudomyrmex gracilis mexicana* Roger and *Pseudomyrmex nigrocincta* Emery).

The experimental part of this study was primarily the comparison of plots containing acacias from which the ants had been removed (by use of insecticides or physical means), with plots containing acacias with their normal ant colonies. Height increment and condition of the shoots were the principal acacia characteristics recorded and compared. These plots were established in vegetation of various ages, and in types of plant communities that are representative of the communities occupied by the majority of the population of *A. cornigera*. The experimental portions of the study were conducted from September 1963 through August 1964, in the lowland coastal plain immediately east of Temascal, in the state of Oaxaca, and in the foothills around Temascal.

It is difficult to evaluate the present experimentation without understanding the bionomics of *A. cornigera* and *P. ferruginea* in more detail than can be gained from the brief discussions in the literature (Belt, 1874; Safford, 1914, 1922; Skwarra, 1930, 1934a, 1934b; Alfaro, 1935; Wheeler, 1913, 1942; Wasmann, 1915). Therefore, the first two sections of this paper are concerned with the bionomics of the acacia and the ant. The depth to which the bionomics of *P. ferruginea* is described is justified from its ecological pertinence and because the bionomics of a pseudomyrmecine ant have not been previously treated in detail. Gathering the bionomic background information began in July 1962, at Campo Cotaxtla (Cotaxtla Experiment Station), state of Veracruz, and continued through October 1964, in Mexico, and at Berkeley, California. Most of the information was obtained in the Temascal area between September 1963 and August 1964. The experimental examination of the ant-acacia interaction is discussed in the third section of this paper.

Other studies and reports in the literature show clearly that the interaction described in this paper is not representative of the relationship between acacias and other ant genera. Furthermore, there is no substantiated evidence that these interactions between other genera of plants and *Pseudomyrmex*, or other genera of ants, are mutualistic. However, there is superficial evidence that there are mutualistic interrelationships between ants and plants, and this is a field worthy of considerable experimental study.

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TERMINOLOGY

Several terms used in this paper must be defined at the outset so as to avoid confusion in their meaning. "Shoot" refers to all of the plant which is above ground, originating from one point on the ground, and does not denote age or degree of branching. "Sucker" refers to the shoot that has recently regenerated from a cut or burned stump. "Seedling" refers to the shoot that has grown from a seed without being cut or burned since the seed germinated. Therefore, a shoot may be either a sucker or a seedling but it includes all of the branches originating from a single point on the ground. Statements about the bionomics of the shoot do not necessarily apply to the root system as well. The various branches are referred to as lateral branches, vertical branches, central axes, or short axillary branches. The "shoot tip" is the terminal 5-15 cm of one of these branches; "axillary tufts" are the clusters of leaves often produced in the axils of swollen thorns after the branch bearing them is over a month old. "Type A" thorns are swollen thorns in the form of a flat V. "Type B" thorns are swollen thorns that are highly twisted; they are usually borne on short axillary branches.

When a shoot is referred to as being "occupied," this means that the outer surfaces of the shoot have more than one or two workers of *Pseudomyrmex ferruginea* on them. Occupied shoots almost invariably have brood in the thorns. An "unoccupied" shoot is one that has essentially no workers on the outer surface of the shoot. There may be workers and/or brood (or founding queens) inside the thorns but the workers may not be active on the surface of the shoot owing to cold weather or small colony size. Both of these conditions are of a temporary nature. A "founding queen" is a queen that is rearing her first brood in a thorn. A "colony queen" is the single queen in a maturing colony. The entire colony may occupy a single shoot, or may be divided among several shoots which can only be reached by trails across the ground or foreign vegetation. The "queen-shoot" is the shoot that contains the colony queen, and the other shoots that contain a part of the colony are referred to as "auxiliary-unit." This type of colony structure is common to many tropical species of *Pseudomyrmex*. A colony may move into a new shoot as a mature colony, or it may develop "in situ" from a founding queen in a thorn on the shoot. The "basal circle" is the area cleared of living foliage under the shoot by an active colony of *P. ferruginea*.

Throughout this paper, the names of collection sites consist of only the precise site. The state and country can be obtained by referring to Figure 6. The plot designations refer to the plots described in the third section of the paper and illustrated in Figure 7. A "plot" is the area that includes the control "subplot" and the experimental "subplot." The vegetation within a plot and immediately surrounding it is relatively uniform in appearance and disturbance regime. The plots are designated by letters; a letter followed by an "A" indicates the plot was abandoned during the study. All subplots numbered "1" (e.g., C-1) are experimental subplots. The last subplot (e.g., C-2, C-3) is always the control subplot.

BIONOMICS OF *ACACIA CORNIGERA*

SYSTEMATICS. The three plants discussed below are the only native swollen-thorn acacias found within the study area. The swollen-thorn acacias in the study area can be recognized by the following diagnoses (adapted from Rudd, 1964), and Figures 1 to 5.

Acacia cornigera (L.) Willd.

Inflorescence two or more times as long as broad; pinnules with costa and secondary venation clearly evident in dried specimens; almost never more than 24 pinnae per leaf; petiolar nectaries elongate trough shaped, from one to eight on mature leaves; yellow to red Beltian bodies on tips of 50-100 percent of leaf segments; short axillary branches bearing slightly to highly recurved thorns that may encircle the branch shaft bearing them; cylindrical legume never dehiscent along a pre-formed suture, sometimes splitting along unpredictable lines following drying, but frequently with thick hard walls that never split.

I recognize the following as synonyms; *Acacia spadicigera* Schl. & Cham., *Acacia cubensis* Schenck, *Acacia nicoyensis* Schenck, *Acacia hernandezii* Saff., *Acacia furcella* Saff., *Tauroceras cornigerum* (Schl. & Cham.) Brit. and Rose, *Tauroceras cornigerum* (L.) Brit. & Rose.

Acacia sphaerocephala Schl. & Cham.

Inflorescence globular to less than one-half again as long as broad; pinnules with costa clearly evident but secondary venation not in dried specimens; almost never more than 24 pinnae per leaf; petiolar nectaries elongate trough shaped, usually only one per mature leaf; yellow to orange Beltian bodies on tips of 50-100 percent of leaf segments; no thorns highly recurved, some with slight twisting along longitudinal axis and shallowly curved tips; cylindrical legume never dehiscent along a pre-formed suture, usually splitting along unpredictable lines following drying, almost never with walls so hard that they cannot be broken by gentle pressure.

I recognize the following as synonyms: *Acacia veracruzensis* Schenck and *Acacia dolichocephala* Saff.

Acacia chiapensis Saff.

Inflorescence a distinct sphere; pinnules with costa clearly evident but secondary venation not in dried specimens; usually over 40 pinnae per leaf and over 80 pinnules per pinna; petiolar nectaries round, eroded cratesiform, one at the base of 30-100 per cent of the pinnal pairs and one to six on the petiole; yellow Beltian bodies usually only on basal two to twelve pinnules of each pinna; no thorns highly recurved or twisted, some on lower trunk of large trees bent back out of plane of thorn "V"; flat legume partly to completely dehiscent along two sutures.

Synonym: *Acacia globulifera* Saff.

In respect to thorn morphology, it is the large volume and the easily removed pith which is of importance to the ant. I propose that the acacias with enlarged thorns that are commonly used as nest sites by ants be called "swollen-thorn acacias" and restrict the name "bull's-horn acacia" and its forms to *Acacia cornigera*. The following species are definitely swollen-thorn acacias: *Acacia cornigera, sphaerocephala, chiapensis, hindsii* Benth., *collinsii* Saff., and *melanoceras* Beur. This terminology provides a common name at the sub-generic level for this group with strongly variable thorn morphology. *A. cornigera* and *A. sphaerocephala* have the same common name in the Spanish language where they occur sympatrically. They are both called *cornizuelo, cuernita, cuernos de toro,* and *cuernitos,* with the first name being nearly universal. Where sympatric in the study area, *A. chiapensis, macracantha* Humb. & Bonpl., and *farnesiana* (L.) Willd. are all called *guisache* in Spanish. The latter two species are not swollen-thorn acacias though they have stipular spines up to 8 cm in length.

Distribution. *A. cornigera* is a widely distributed plant. At present, it has been collected from northeastern Mexico south to the Isthmus of Tehuantepec across the Isthmus and thence south to the province of Guanacaste in Costa Rica. It also has a patchy distribution on the Yucatan Peninsula and eastern Guatemala. *A. sphaerocephala* is more restricted; it has been found in the coastal lowlands along the northern edge of the range of *A. cornigera* and around the city of Veracruz, Mexico (Fig. 6). Within the study area, *A. chiapensis* is very local in distribution, having been collected only in eastern Oaxaca and southeastern Veracruz (Fig. 6).

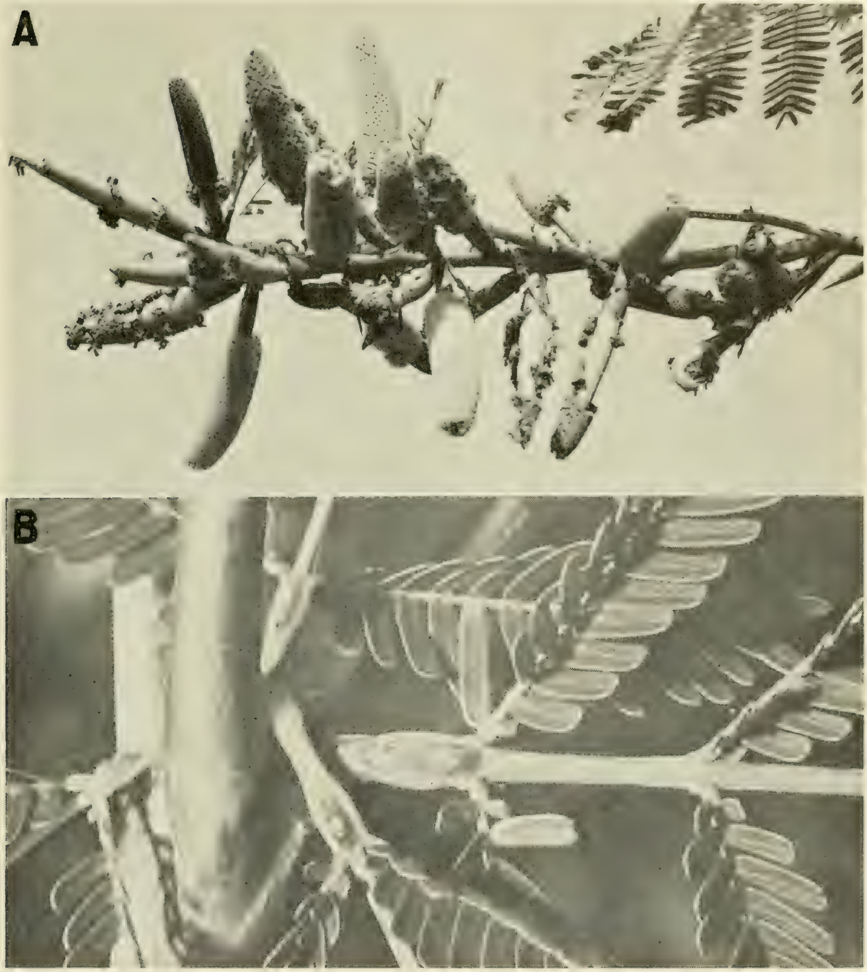


FIG. 1. a. A flowering branch of *Acacia cornigera* with flowers unopened, opened, and shedding dead florets. The shoot was three years old, 3 m tall, and growing in brushy pasture 7 km east of Temascal. Photo 17 Jul. 1964. b. Foliar nectaries of *Acacia cornigera* on a tuft of axillary leaves from the axil of a type A thorn that has lost its leaf. Same shoot as that in Fig. 1a. Photo 17 Jul. 1964.

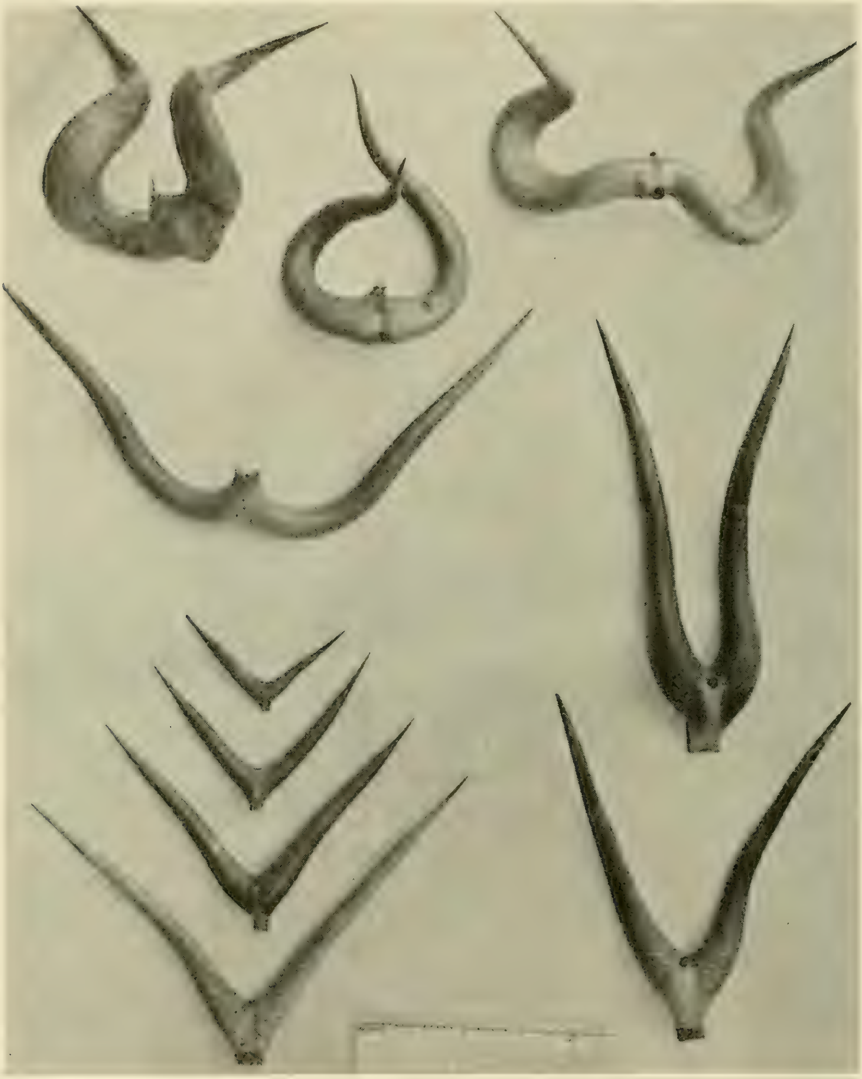


FIG. 2. Swollen stipular thorns taken from *Acacia cornigera.* The upper three twisted thorns are classified as type B, the middle two as type AB, and the lower five as type A. All the thorns are from the shoot in figure 1a. This range of thorn variation is characteristic of thorns from occupied shoots over two years old. Photo 17 Jul. 1964.

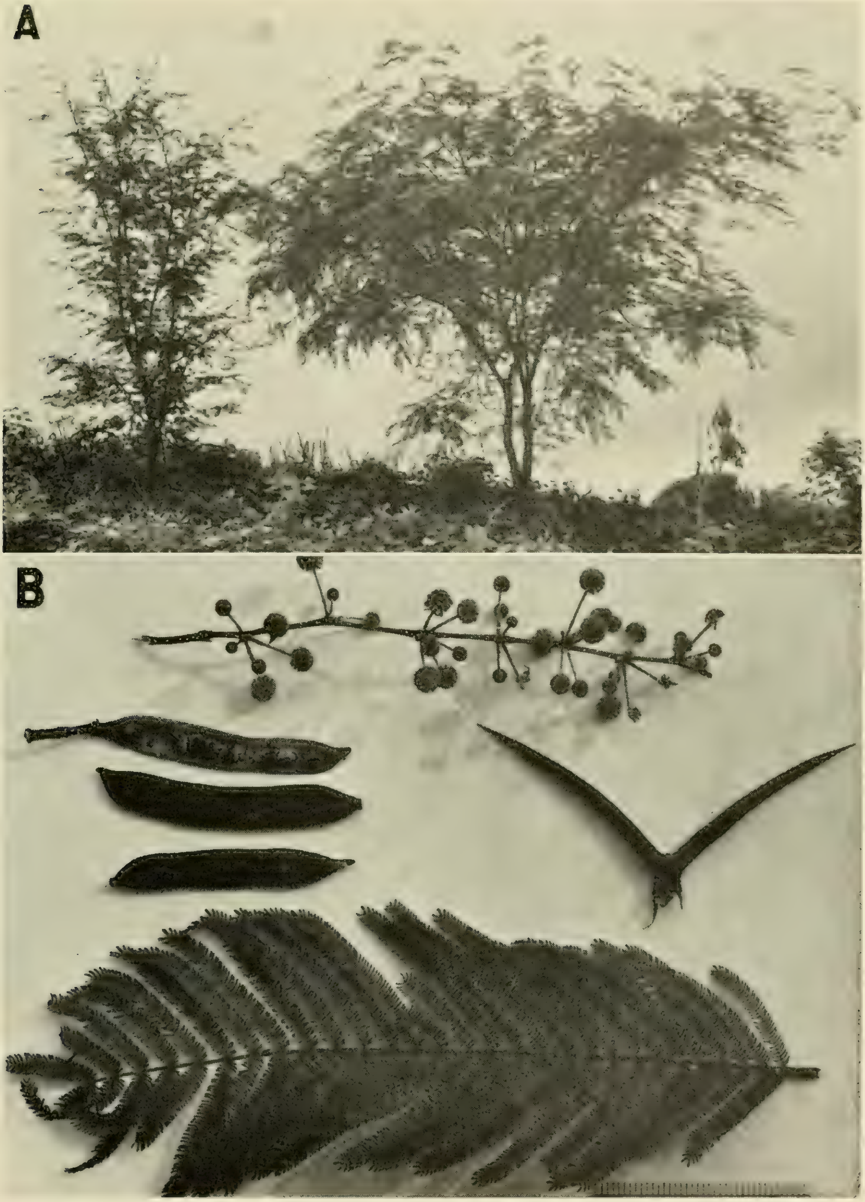


FIG. 3. a. Two mature shoots of *Acacia chiapensis.* The narrow shoot is representative of that portion of the population that resembles *Acacia cornigera,* and it is occupied by *Pseudomyrmex ferruginea.* The spreading shoot is representative of that portion of the population that resembles *Acacia macracantha*; it is not occupied. Both shoots are about 6 m tall, and 5-6 years old. Shoots growing on the roadside 0.5 km west of Temascal. Photo 3 Jul. 1964. b. Flowering branch, legumes, leaf, and type A thorn from *Acacia chiapensis.* Collected from the right-hand shoot in Figure 3a on 12 Jun. 1964.

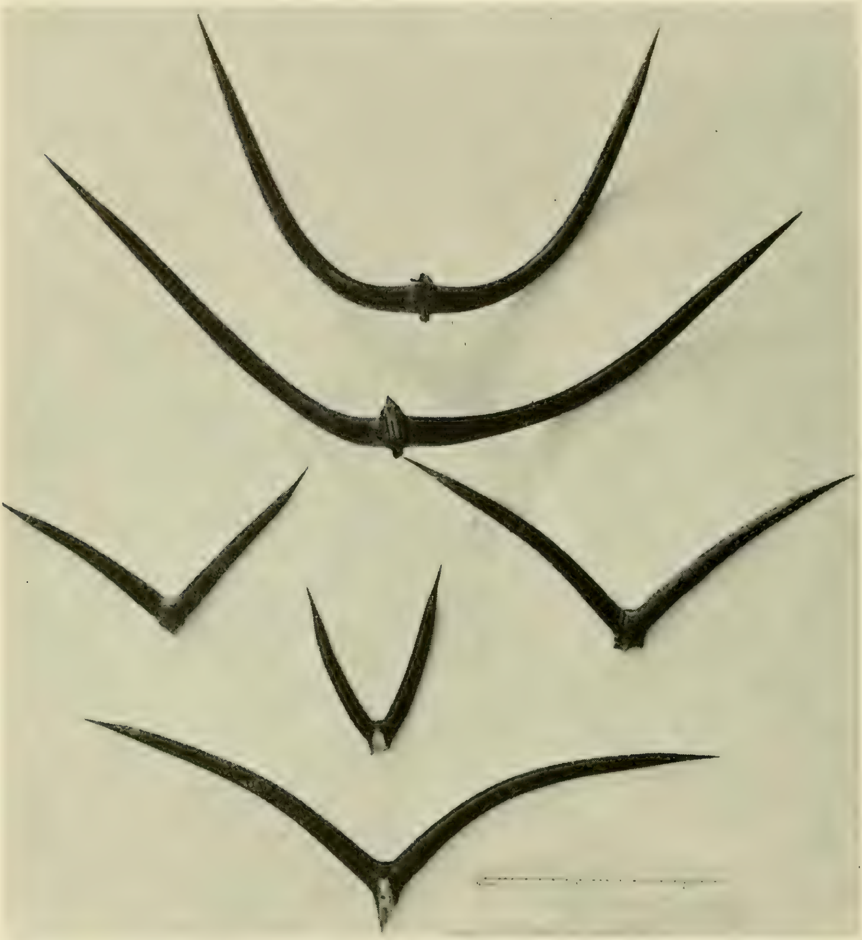


FIG. 4. Swollen stipular thorns from *Acacia chiapensis*. The upper two thorns should be classified as type B since they came from short axillary branches on the main trunk and are slightly recurved. The lower four thorns are type A from long lateral branches. All of these thorns came from a shoot 11 m tall that was representative of that portion of the population that resembles *Acacia macracantha* (see Fig. 3a). Shoot growing on the roadside 0.5 km west of Temascal.

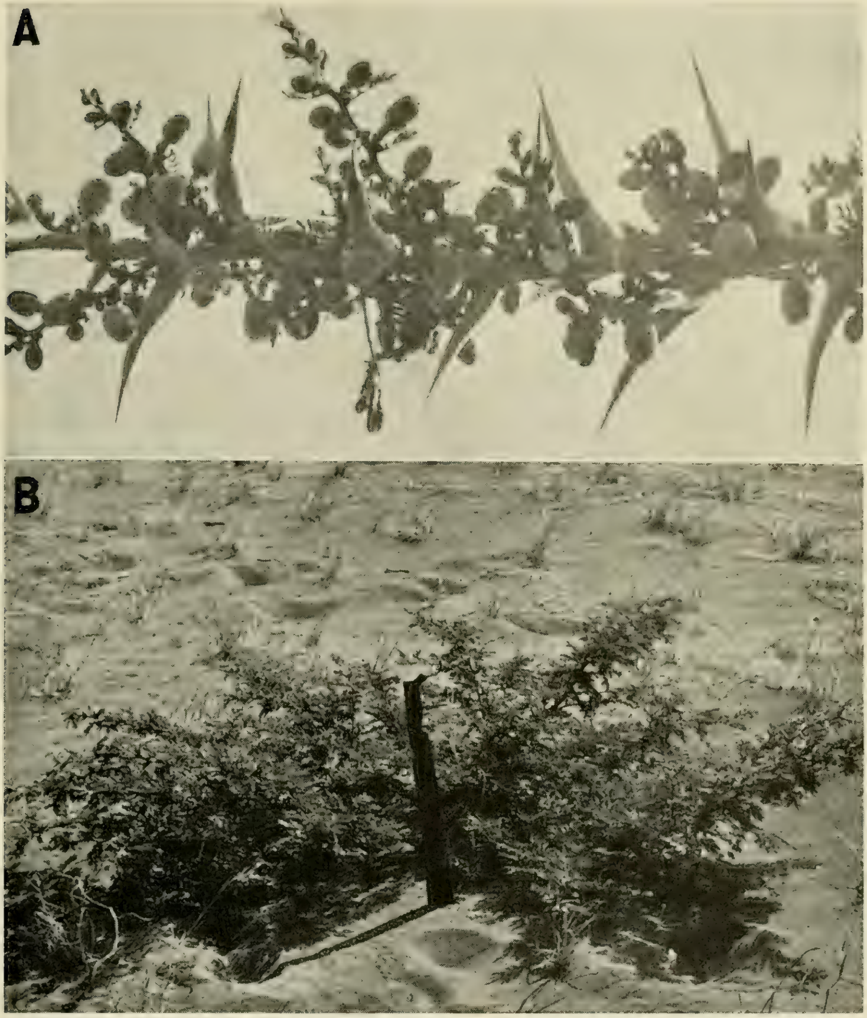
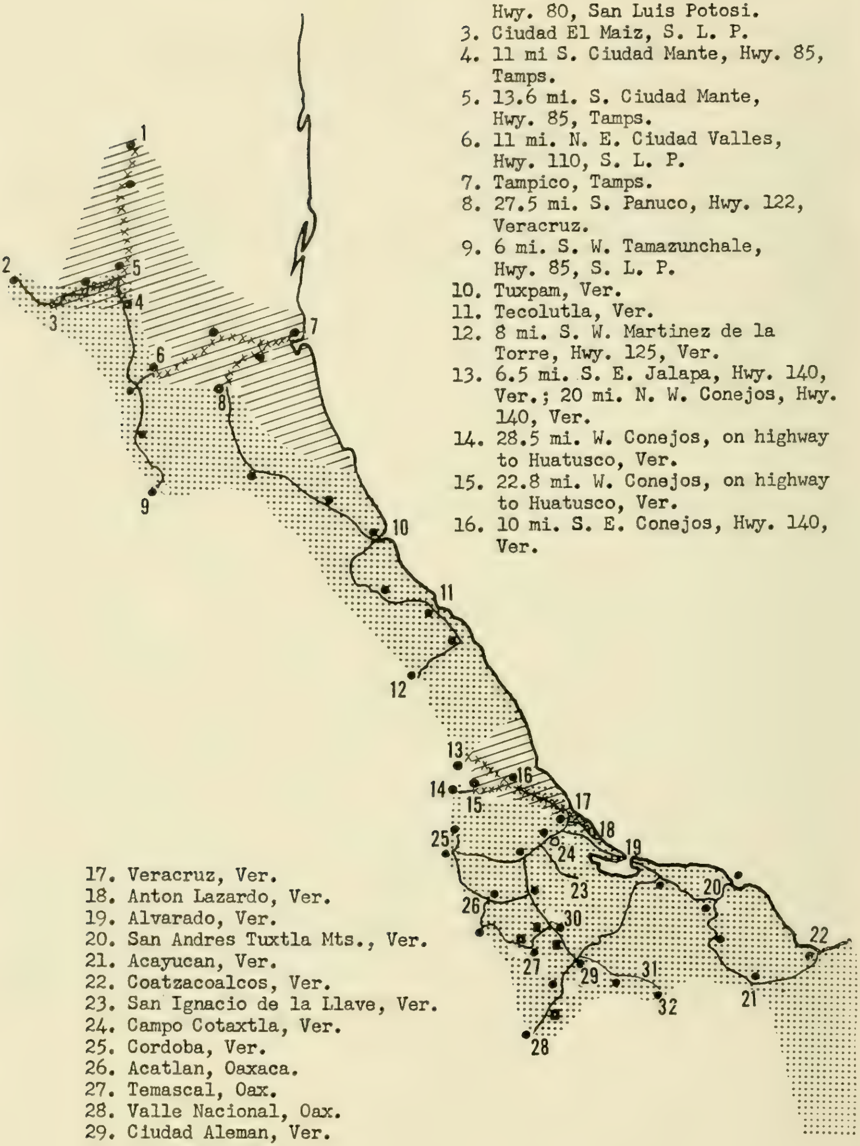


FIG. 5. a. A lateral branch with flowering branches of *Acacia sphaerocephala.* Taken from a 2 m tall roadside shoot growing at the northern margin of its geographic distribution (4 km south of the point where highway 85 crosses the Tropic of Cancer, Tamaulipas, Mexico). Shoot leafless except for small leaves on the flowering branches. Photo 4 Mar. 1964. b. Mature shoot of *Acacia sphaerocephala.* Growing 25 m back from the high tide level on the beach 9 km north of Anton Lazardo, Veracruz, Mexico. This shoot was occupied by *Crematogaster* sp. and is representative in life form of those shoots growing on the sand dunes 20-3000 m of the ocean. At inland sites, *Acacia sphaerocephala* is very similar in life form to *Acacia cornigera.* Photo 22 Dec. 1963.



1. Hwy. 85 at the Tropic of Cancer, Tamaulipas.
2. 20 mi. N. W. Ciudad El Maiz, Hwy. 80, San Luis Potosi.
3. Ciudad El Maiz, S. L. P.
4. 11 mi S. Ciudad Mante, Hwy. 85, Tamps.
5. 13.6 mi. S. Ciudad Mante, Hwy. 85, Tamps.
6. 11 mi. N. E. Ciudad Valles, Hwy. 110, S. L. P.
7. Tampico, Tamps.
8. 27.5 mi. S. Panuco, Hwy. 122, Veracruz.
9. 6 mi. S. W. Tamazunchale, Hwy. 85, S. L. P.
10. Tuxpam, Ver.
11. Tecolutla, Ver.
12. 8 mi. S. W. Martinez de la Torre, Hwy. 125, Ver.
13. 6.5 mi. S. E. Jalapa, Hwy. 140, Ver.; 20 mi. N. W. Conejos, Hwy. 140, Ver.
14. 28.5 mi. W. Conejos, on highway to Huatusco, Ver.
15. 22.8 mi. W. Conejos, on highway to Huatusco, Ver.
16. 10 mi. S. E. Conejos, Hwy. 140, Ver.

17. Veracruz, Ver.
18. Anton Lazardo, Ver.
19. Alvarado, Ver.
20. San Andres Tuxtla Mts., Ver.
21. Acayucan, Ver.
22. Coatzacoalcos, Ver.
23. San Ignacio de la Llave, Ver.
24. Campo Cotaxtla, Ver.
25. Cordoba, Ver.
26. Acatlan, Oaxaca.
27. Temascal, Oax.
28. Valle Nacional, Oax.
29. Ciudad Aleman, Ver.
30. La Granja, Ver.
31. Villa Azueta, Ver.
32. 10 mi. E. Villa Azueta, Ver.

FIG. 6. The distribution of *Acacia cornigera, Acacia sphaerocephala,* and *Acacia chiapensis* within the study area. The range of *Pseudomyrmex ferruginea* is congruent with the range of these three acacias except for a narrow strip along the dunes to the south of the city of Veracruz. Solid lines indicate roads along which *Acacia cornigera* has a population density of at least one plant per ten linear miles. Lines of "X" indicate roads along which there is at least one *Acacia sphaerocephala* per ten linear miles. Collection sites are indicated by solid squares for *Acacia chiapensis* and solid circles for *P. ferruginea.* Fine stippling represents the postulated continuous distribution of *A. cornigera* occupied by *P. ferruginea.* Diagonal striping represents the postulated continuous distribution of *A. sphaerocephala* occupied by *P. ferruginea.* Only landmarks and key localities are listed.

Observations were made in many parts of the study area. Experimentation was done at Campo Cotaxtla, and the Temascal-La Granja area (Fig. 7). Unless otherwise indicated, the discussions in this paper are believed to be representative of the *A. cornigera* and *P. ferruginea* populations in the study area. *P. ferruginea* was found to be relatively uniform in behavior, morphology and colony structure throughout the study area. *A. cornigera* showed some morphological and behavioral variation that was apparently associated with different habitats and distributional discontinuities. Visits were made to the following areas within the study area; Coatzacoalcos (Mar.); San Andres Tuxtla and Tlacotalpan (Dec., Mar.); Tuxtepec (Oct.); Veracruz, Cordoba, and Jalapa (Sept., Dec., Jan., Mar., Apr.); Tamazunchale and Tampico (Jan.); and Cuidad Victoria (Mar.).

GROSS MORPHOLOGY. In the following discussion of the morphology of *Acacia cornigera,* only those aspects which are of direct importance to the understanding of the ant-acacia interaction have been elaborated.

Mature shoot. Figures 8-15 show representative stages in the development of a sucker shoot of *A. cornigera.* At the time of flowering, the shoot may be nine months to 15 years old. The shrub or small tree has a life form which is in great part dependent upon the physiognomy of the surrounding plant community, the age of the shoot, the phytophagous insects present during the rainy season, and the effectiveness of the ant colony in removing damaging organisms. It usually has one main trunk and this is often developed from an old root stock left after cutting or burning. In open pastures and on riverbanks, it is often of spreading habit and less than 5 m tall (Fig. 13). Where competing with surrounding vegetation for light, it is usually emergent with a long thin trunk (Fig. 14-15). In second growth vegetation, occupied shoots of *A. cornigera* continue to stay at the general canopy level or above until the competing species heights have reached 12-20 m. At this time, *A. cornigera* has a D.B.H. of 14-18 cm. When heavily shaded, the shoots rarely grow over 2 m in height and are then very slender (Fig. 21a). When the ruteline scarab *Pelidnota punctulata* Bates and the larvae of the noctuid moth *Coxina hadenoides* Guen. are common, their persistent removal of the shoot tips of certain occupied shoots during the rainy season produces flat-topped, thick canopied shoots. In most plant communities, phytophagous insects are sufficiently abundant during the rainy season so that they severely stunt the growth of unoccupied *A. cornigera* by destroying mature foliage and shoot tips.

The growth pattern is affected by the same factors that affect the life-form of *A. cornigera.* During the first three months to a year, shoots from old root stocks characteristically lack long lateral branches; vertical growth of the main axis is emphasized. The extent of later growth of lateral branches is associated with the amount of light received by the part of the crown

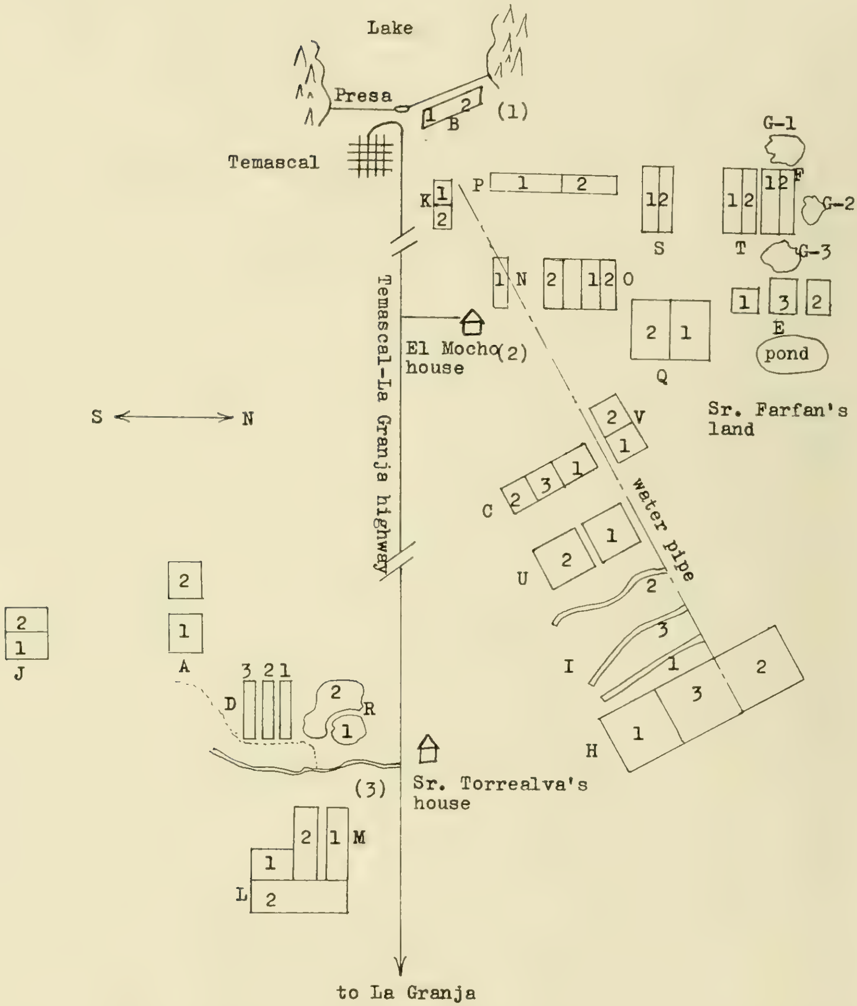

Lake
Presa
(1)
B
1
2
Temascal
G-1
F
G-2
G-3
P
K
S
T
E
pond
N
O
Q
Temascal-La Granja highway
El Mocho (2)
house
S
N
Sr. Farfan's
land
V
C
U
water pipe
I
H
J
A
D
R
(3)
Sr. Torrealva's
house
M
L
to La Granja

FIG. 7. Diagrammatic representation of the experimental plots and subplots established in this study between Temascal and La Granja. Area (1) lies to the north of Temascal and below the earth-fill dam, the Presa Miguel Aleman. Area (2) is on Señor Farfan's land around and behind El Mocho's house. Area (3) lies across the road from Señor Torrealva's house. The plots are not drawn to scale; for dimensions see the plot descriptions.

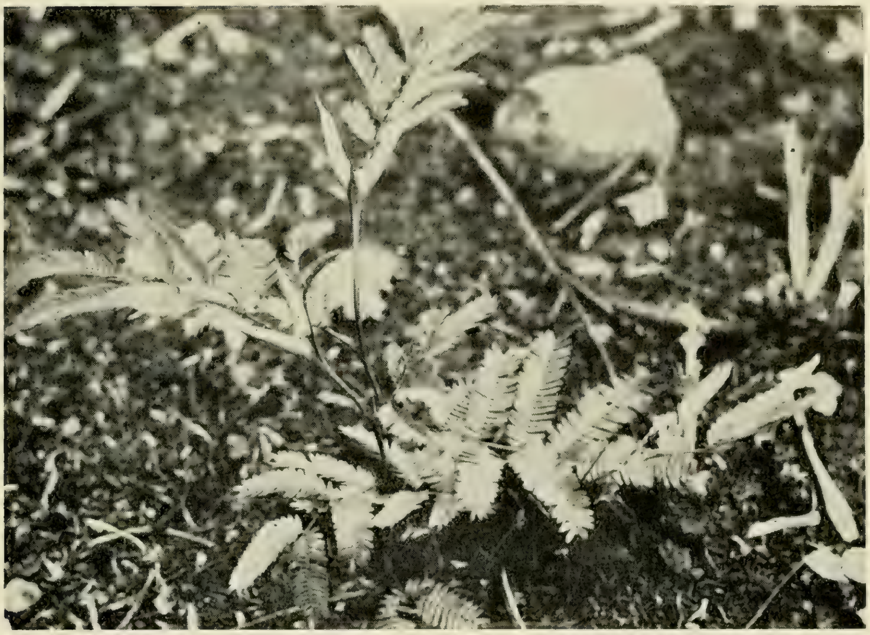


FIG. 8. A pair of 21 day old sucker shoots from a 14 mm diameter burnt stump of *Acacia cornigera* in a pasture burned 32 days previously on 1 Dec. 1963. Each thorn contains a founding queen. The uppermost shoot tip is eaten off by a larva of *Coxina hadenoides* while the lower one is undamaged. The shoot is 15 cm tall and growing 7 km east of Temascal.

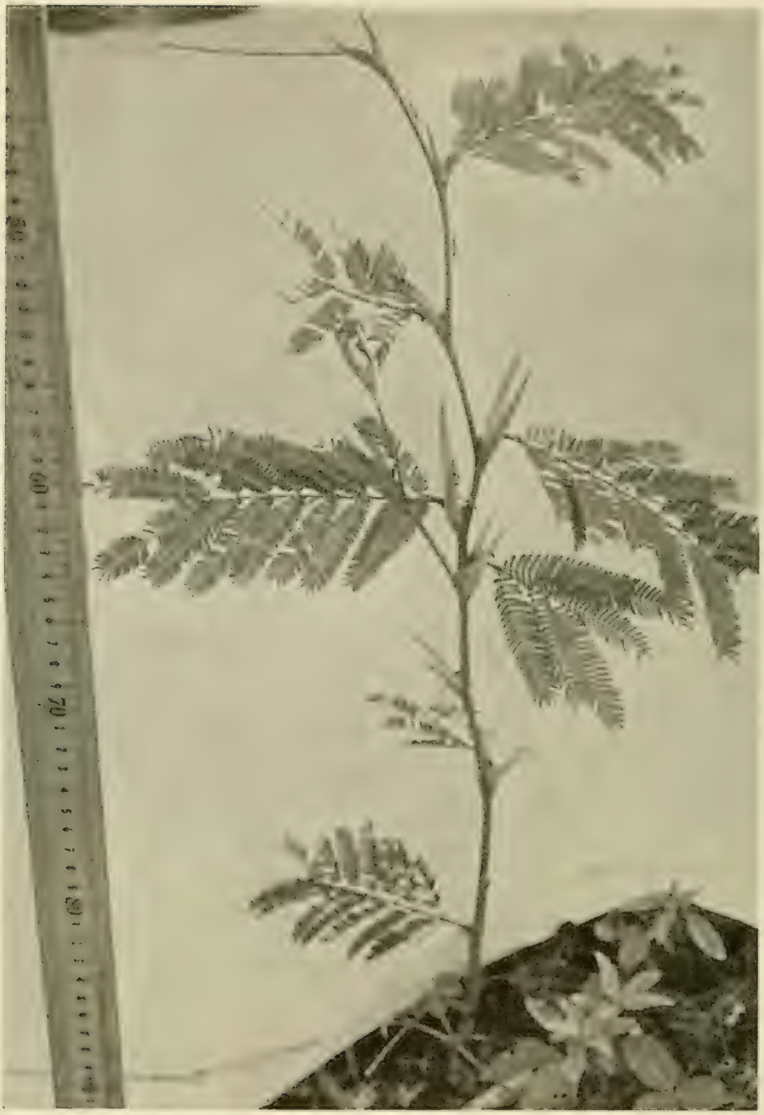


FIG. 9. Unoccupied 5 month old sucker shoot of *Acacia cornigera* growing in an area that was burned in May 1963, 7 km east of Temascal. Each thorn contains a founding queen, and five founding queens of *Pseudomyrmex ferruginea* can be seen on the outside of the shoot. Four hours after sunrise, this shoot had the exceptional number of 31 founding queens on it outside of the thorns. A larva of *Halisodota* sp., probably *H. pura,* was observed to eat out the damaged green thorn on the short lateral branch. The upper terminal shoot tip was eaten by an unidentified insect; its mandibular scars are visible on the right hand half of the terminal thorn. The founding queen near the apex of the fourth swollen thorn from the base is attempting to pull the occupant founding queen out by her antenna. Photo 10 Oct. 1963.

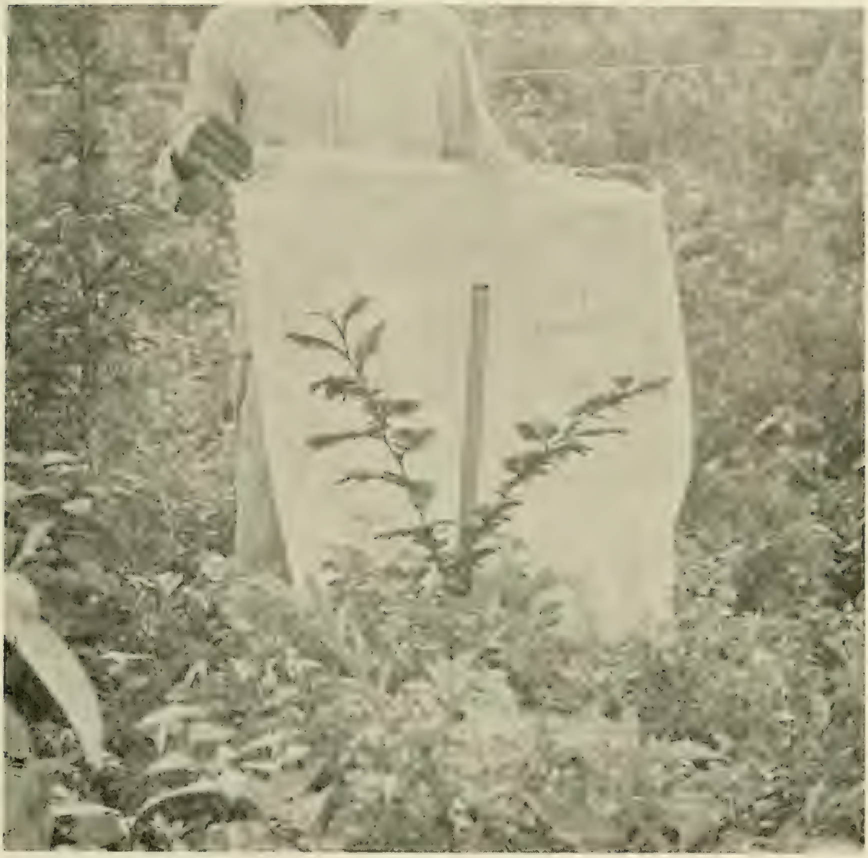


FIG. 10. An occupied 5 month old shoot of *Acacia cornigera* growing in vegetation that was cut but not burned in late May 1963 (plot P). It was 97 cm tall. This is an auxiliary-shoot of the queen-shoot 70 cm to the left that was cut at the same time. Of the 37 type A thorns on this shoot, 29 contained brood and workers of *Pseudomyrmex ferruginea,* and there were approximately 400 workers on the shoot. The surrounding vegetation is almost entirely sucker shoots from old root stocks of *Croton miradorensis, Tournefortia hirsutissima, Eupatorium odoratum* and Leguminosae, and annual *Solanum torvum* and Labiatae. Photo Oct. 1963.

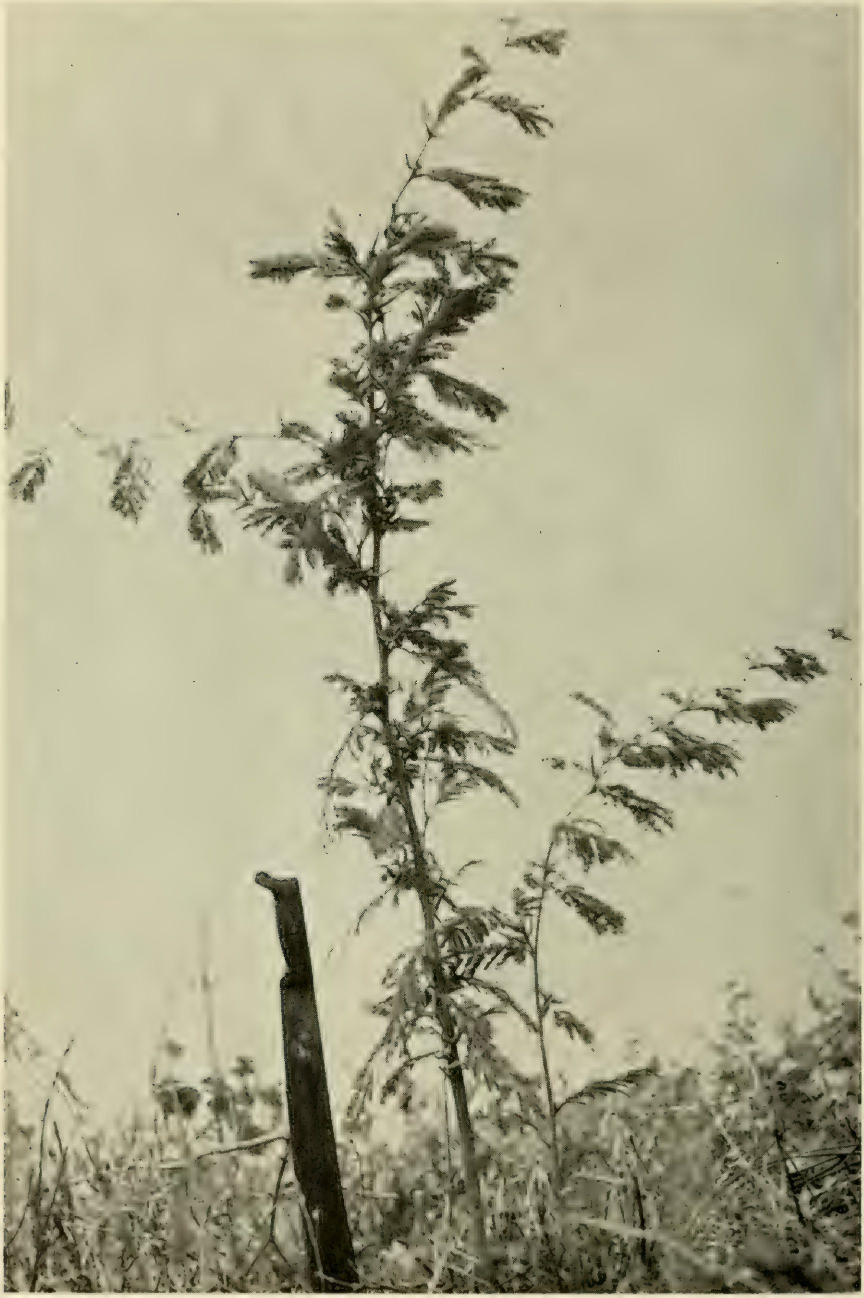


FIG. 11. An occupied 15 month old shoot of *Acacia cornigera* (near plot P). It was 164 cm tall. The surrounding vegetation was 95 cm tall but was cleared to expose the shoot. The shorter shoot to the right is a four month old auxiliary-shoot with 161 workers, while the queen-shoot had 1,686 workers on and in it. Photo 26 Mar. 1964.

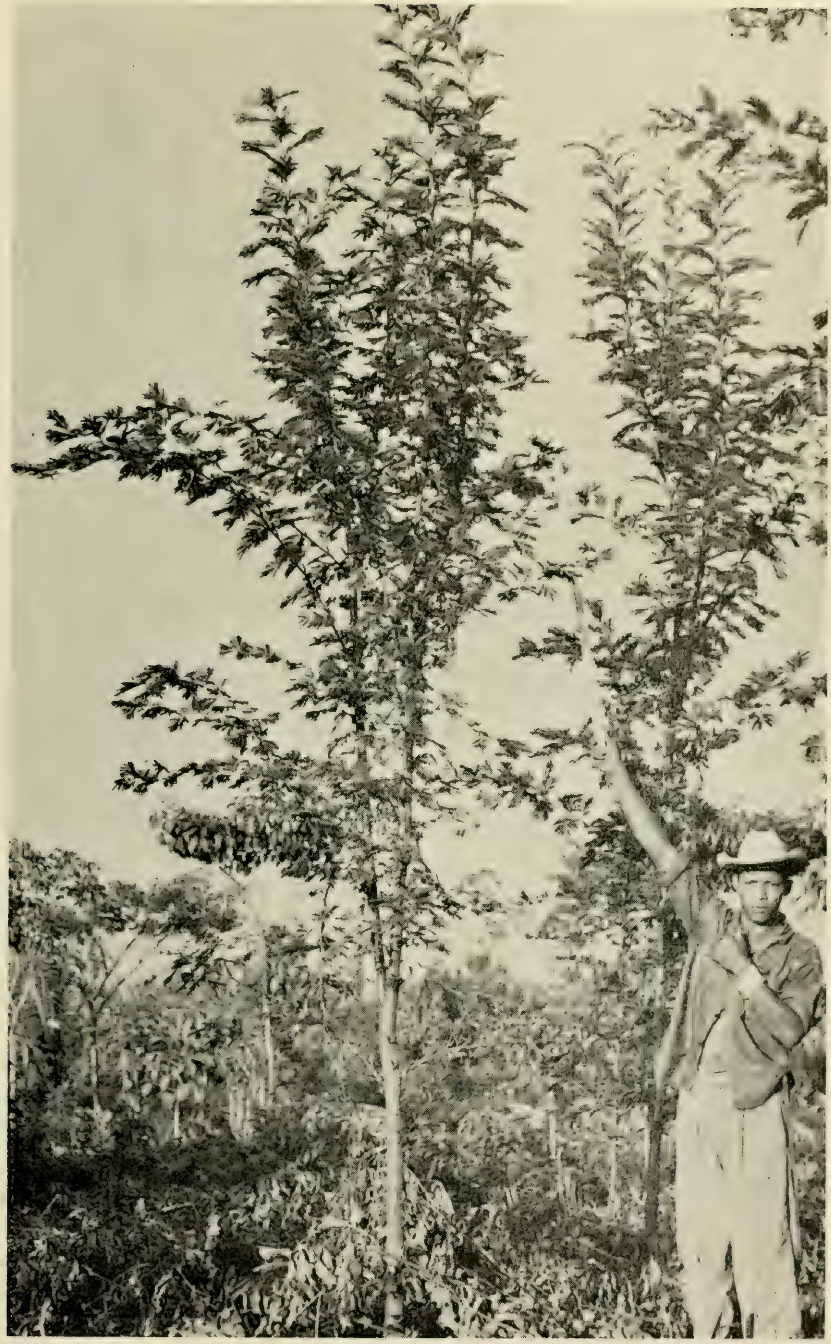


FIG. 12. An occupied 17 month old sucker shoot of *Acacia cornigera* in subplot E-3 before treatment. It was 4.5 m tall. The surrounding vegetation was about 3 m tall but was cleared to fully expose the shoot; it was composed of *Bixa orellana, Croton glabellus, Jatropha urens, Cassia bicapsularis,* many species of woody vines, and other less common shrubs. The shoot on the right is of the same age and history as the central one. Shoots of this size usually contain a queen-unit with about 10,000 workers by the end of their second growing season. Photo late Sept. 1963.

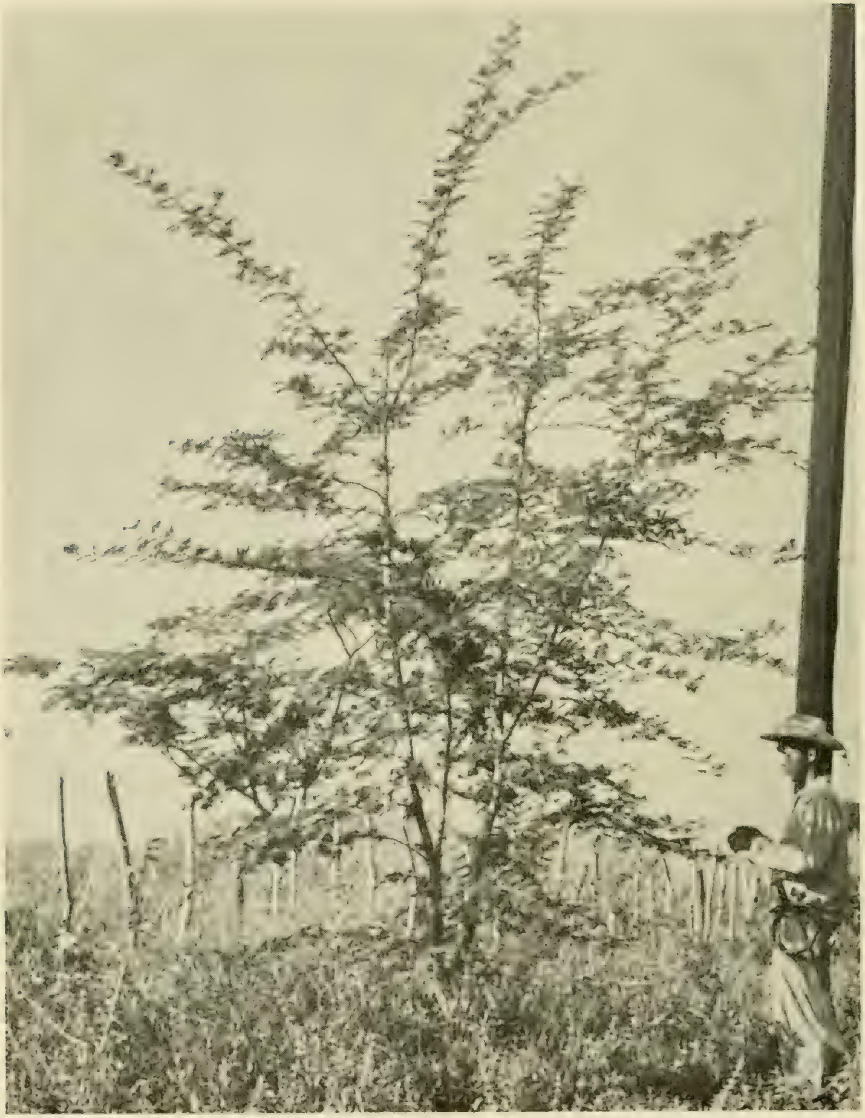


FIG. 13. An occupied 4 year old shoot of *Acacia cornigera.* It was 520 cm tall. This shoot had apparently produced all of its growth in a heavily browsed and grazed pasture. A three year old shoot of this size contained a colony of *Pseudomyrmex ferruginea* with 12,269 workers. Directly in the center of this shoot is a recently vacated nest of *Ptangus sulpheratus,* the Derby Flycatcher. Photo early Oct. 1963 in a pasture 3 km west of Las Tinajas, Veracruz, Mexico.

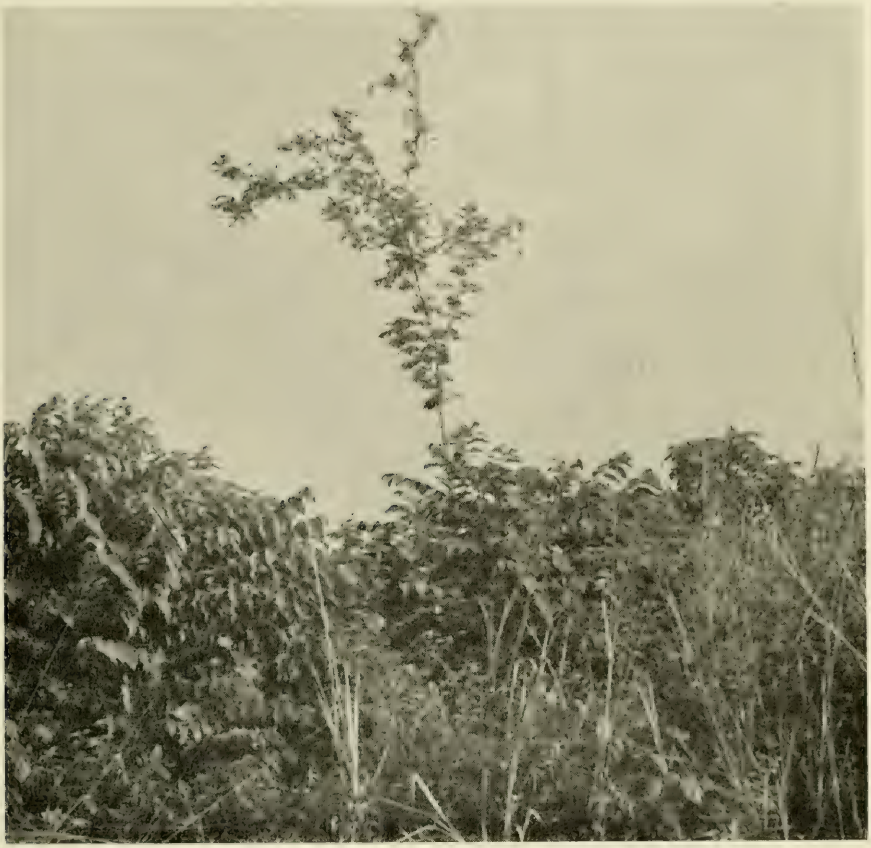


FIG. 14. An occupied 4 year old emergent shoot of *Acacia cornigera* in subplot V-2. It was 7 m tall and a queen-shoot with 9,257 workers. This shoot produced its growth in vegetation that was ungrazed after the first year after it was cut. The surrounding vegetation is mostly Compositae, *Guazuma ulmifolia, Helicteres guazumifolia, Tabebuia pentaphylla, Cassia bicapsularis,* Malvaceae, and other shrubs and trees. Photo late Sept. 1963.

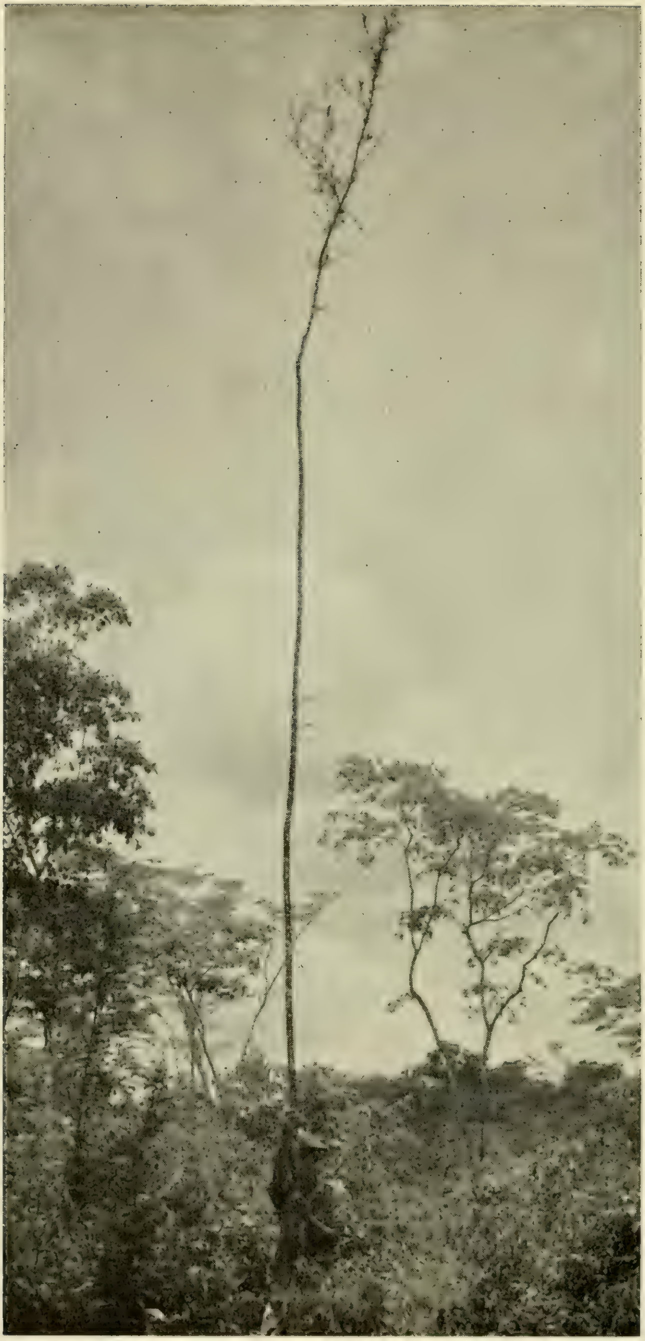


FIG. 15. An unoccupied 7 year old shoot of *Acacia cornigera* removed from 8 year old regeneration east of subplot H-1. It was 11 m tall. This shoot's canopy was about 50 cm below the general canopy of the vegetation from which it was removed. It had 39 mature leaves and no intact shoot tips. This shoot would have probably died within the next year although its stump produced quite vigorous sucker growth. The straight and slender trunk with naturally pruned branches is characteristic of shoots that have developed in ungrazed and unburned regeneration. Photo early Jul. 1964.

producing the branches. The axis of an elongating branch is bright green down to the fifth to tenth swollen thorn. A dark green photosynthesising layer is present, and usually externally visible, beneath the extremely thin epidermis over most of the shoot. It is probable that photosynthesis under the epidermis constitutes a significant portion of that of the shoot as a whole, especially during the dry season when the shoot may bear as few as 5 per cent of the number of leaves present during the rainy season. *A. cornigera* is quick to respond to light; this is shown by the many trees whose shoot tips have bent toward a hole in the canopy and then grown up through it. The wood of trees over 3 months old is tough and springy. During the first two years of growth, leaves are usually produced nearly to ground level; other species of trees and tall shrubs of the same height in the same plant community usually have leaves only on the uppermost part of the shoot. In dense vegetation the production of leaves low on the shoot by *A. cornigera* is most strongly associated with the pruning activities of *P. ferruginea* workers; this pruning often allows sufficient light penetration for the leaves of *A. cornigera* to be functional below the canopy of the surrounding vegetation. Dead branches, and thorns over three months old, are usually shed.

The short flower-bearing branches (Fig. 1a) are produced during the middle of the dry season but contribute little to the form of the shoot. These branches have small leaves with fewer pinnae, do not develop swollen thorns, and die after the seed crop (Fig. 16) has fallen during the following dry season.

The roots have numerous nodules; these are first obvious when the seedling is about three weeks old and has three to five leaves. A three year old root system may have a tap root over 3 m long. In wet areas, lateral roots are well developed and vertical shoots sometimes develop from them. Root stock cleaned of all its shoots can be transplanted and produces healthy shoots. Root grafting has not been ascertained.

Leaf. The dark green, bipinnate leaves (Fig. 17) show high variation in numbers of pinnae and pinnules per leaf on the same shoot. A representative leaf has 10 pinnae and 300 pinnules. A leaf of this size (18 cm long) is usually subtended by a large swollen stipular thorn and is on a long lateral branch or the main axis (Fig. 9). Small leaves are produced in tufts in the axils of swollen thorns, or on flowering branches, especially during the dry season.

As a result of the annual leaf drop, rapid vertical growth, and lack of retention of large branches, there are rarely over 600 leaves on a shoot. During the first year of growth from a stump, a shoot occupied by a large colony of *P. ferruginea* produces about 300 leaves. This number is most commonly reduced by two types of defoliation. The larvae of the syssphingid *Adelocephala mexicana* Bsdv. may eat nearly all of the mature leaves from a shoot

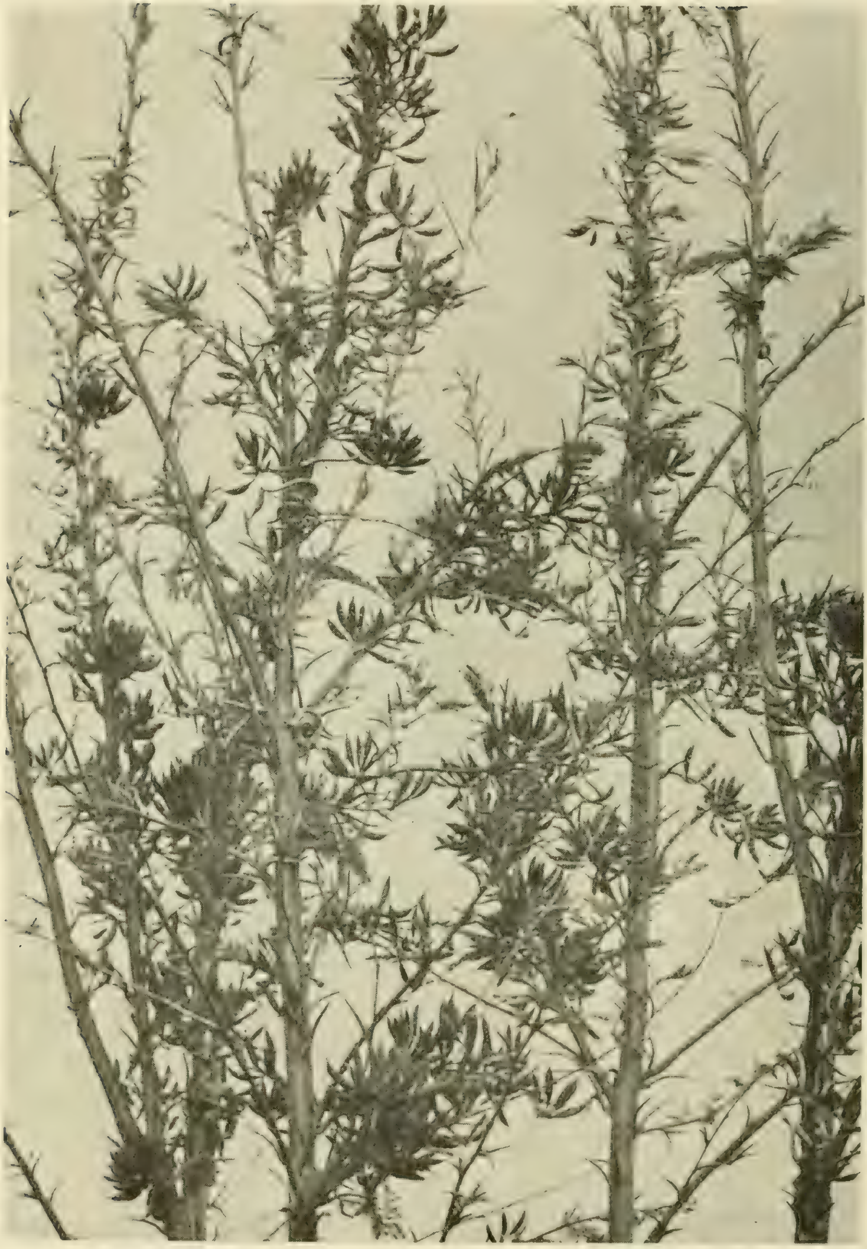


FIG. 16. A section of the canopy of a mature shoot of *Acacia cornigera* with a normal heavy seed crop. This shoot was 4 m tall and growing in a bushy pasture 1 km north of Temascal. Photo 26 May 1964, after the rains had started, but before this shoot had responded by producing new shoot tips.

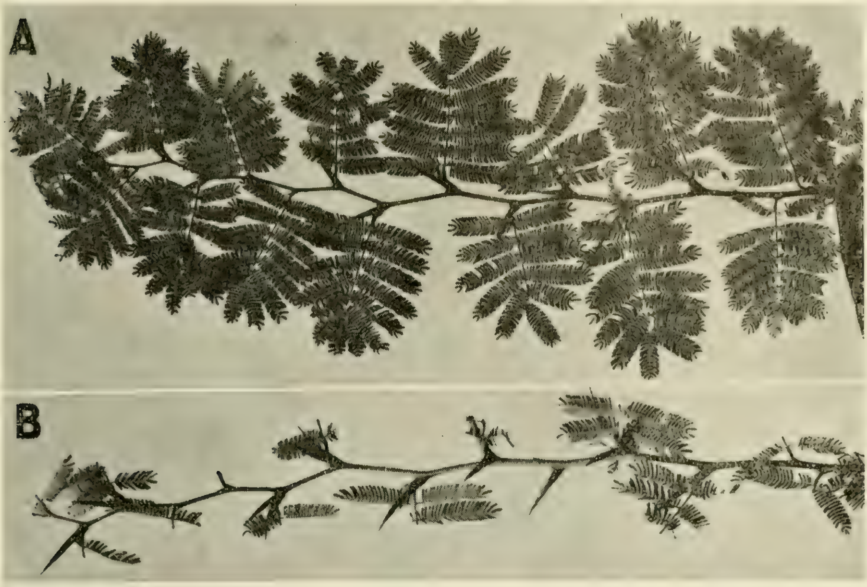


FIG. 17. a. Lateral branch from an occupied shoot of *Acacia cornigera.* While the shoot tip is still intact, this branch has nearly ceased lateral extension. Note that the leaves project well past the ends of the thorns. b. The same lateral branch as in Fig. 17a, but 5 minutes later, after a tame Brocket Deer (*Mazama americana temama;* temazate) had browsed the hand-held branch (worker ants had been removed from the outside of the branch). Photo 20 Jul. 1964, of a branch from a roadside shoot growing 18 km east of Temascal.

in the 1-2 m height range, but is deterred through attack by *P. ferruginea,* from destroying the shoot tips. In cases where all of the shoot tips have been removed from an occupied shoot, the adults of the rutelline scarab *Pelidnota punctulata* or the larvae of the noctuid moth *Coxina hadenoides* are usually responsible. There is a subsequent severe reduction in leaf production until new shoot tips are initiated.

In the Temascal area, the pattern of leaf drop of *A. cornigera* differs in some respects from that of other deciduous plants. Nearly all leaves produced during the rainy season of the previous year are gradually dropped during the warm and dry season (Mar.-May). Leaf drop begins with the oldest leaves and gradually moves upward. Therefore, the growth since the end of the last dry season can be identified as that above the first swollen thorn with its subtended leaf still present. The shoot is rarely leafless, and the length of time without leaves varies greatly among individuals. Though little lateral and vertical growth occurs during the dry season, a few axillary leaf tufts are continually produced on shoots over a year old and flowering branches with small leaves are produced in the middle of the dry season.

The time of production of the new crop of leaves varies with the age of the shoot and the individual plant. Shoots less than a year old have only partial leaf drop during the dry season and shoots less than six months old usually have no loss of leaves. The new period of rapid vertical growth starts during the last one to two months of the dry season in plants under one year of age. In these shoots the new branches are often produced from a thorn axil nearly at the top of the shoot and growing upward, immediately produce a height increment as well. On the other hand, shoots over a year old begin vertical growth near the time of the first rains. This growth is in the form of vertical branches from thorn axils well below the tips of the highest of the previous year's branches, but still at or above the level of the surrounding canopy of other species of plants; there must be several weeks to a month of growth before a height increment can be recorded.

The shoot tip of *A. cornigera* differs in several important ways from that of acacias not inhabited by ants. It is glabrous and slightly sticky; the workers of *P. ferruginea* lick off this sticky material and thus aid in the separation of the pinnules. While the two terminal unexpanded leaves are clasped tightly over the shoot apex as is the usual case in Central American acacias, the terminal portion of the shoot tip is extremely fragile and can be broken off by bending or snapping with the finger; the shoot tips of *Acacia macracantha, Acacia farnesiana* and the pale-leafed form of *Acacia chiapensis* are very tough and fibrous. The shoot tip of *A. cornigera* is bland to pleasant tasting to humans in contrast to that of *acacia* spp. not associated with ants. In the latter, the shoot tips are very bitter tasting.

Beltian bodies. The oval to tear-drop shaped Beltian bodies are the modified ends of the leaf segments (Fig. 18) that are borne one to the tip of each pinnule, pinna, and leaf rachis. This omnipresence generally applies only to shoots over 1 m tall growing in full sunlight. The Beltian bodies are usually removed within five days of their appearance by *P. ferruginea* workers on occupied shoots, or after some indeterminate period by *P. ferruginea* founding queens, *P. gracilis mexicana* or *Solenopsis geminata* Fabricius (rarely) on unoccupied shoots. They are cut up by the *Pseudomyrmex* species and fed to the larvae. Due to the continual harvesting activity on occupied shoots, Beltian bodies are usually found only on new shoot tips.

During the first two months of the rainy season, groups of shoots occupied by one *P. ferruginea* colony sometimes produce more Beltian bodies (new foliage) than the colony will harvest. In this case, many of the leaves retain their pinnule-end Beltian bodies because the *P. ferruginea* colony does not allow other possible harvesters on the shoot. Beltian bodies on the ends of pinnae and the leaf rachis are always harvested if the shoot is occupied. Depending on the weather, those that are not harvested eventually dry and drop off, or rot.

No direct use to the plant of Beltian bodies is postulated in the literature. They were regarded by F. Darwin (1877) and Schimper (1888) as homolo-

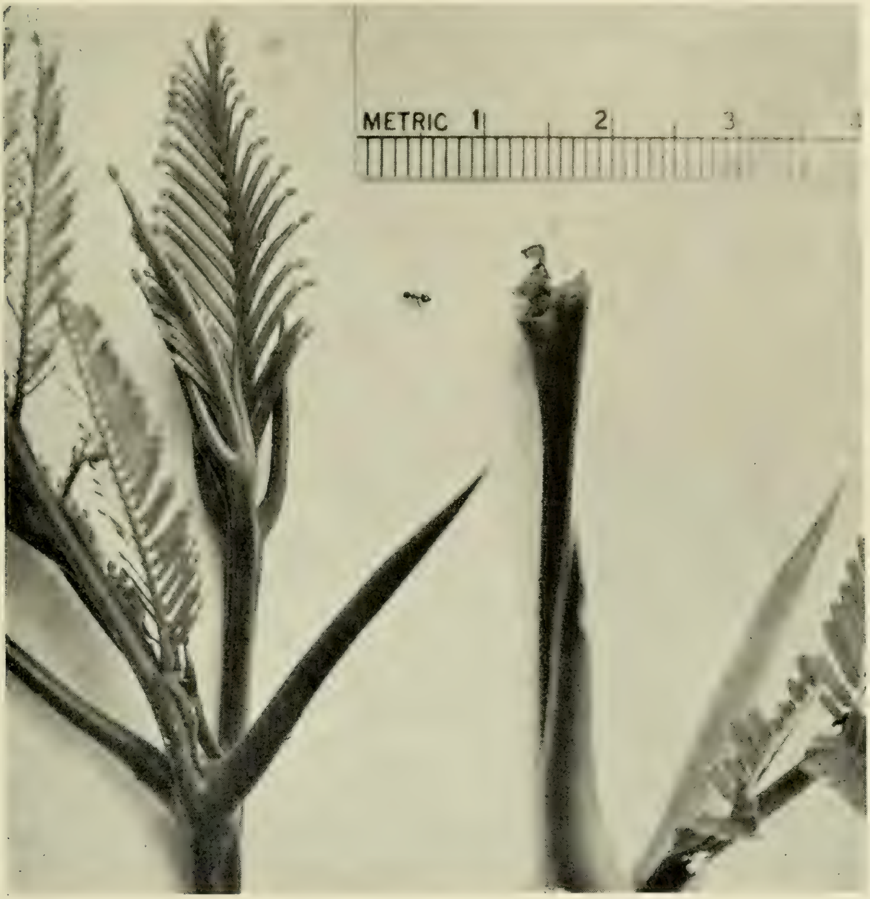


FIG. 18. Two shoot tips of *Acacia cornigera* from plot N. The left-hand shoot tip is undamaged and was taken from an unoccupied shoot; the unharvested Beltian bodies on the ends of the raches and pinnae are mature (ripe) while the Beltian bodies on the pinnules are not yet expanded. The right-hand shoot tip was eaten off by *Coxina hadenoides*; the shoot from which it was taken was occupied by *Crematogaster* sp., one of which is walking between the shoot tips. Photo June 1964.

gous to serration-glands on the leaf margins of other plants. Preliminary examination indicates clearly that they are modified ends of the leaf parts, and that the rachis extends out into them. Darwin considered that they were full of oils and proteins. Preliminary experiments to determine the food value of Beltian bodies indicate that they are similar to yeast in quantity and quality of nutrients. This degree of nutritive value of foliar tissue is unusual (H. T. Gordon, personal communication). About 3000 Beltian bodies ripen on a 2 m tall occupied tree per day during the first three months of the rainy season; this means about 450 mg of solid food per day is available to the ant colony. With the exception of several species that require considerable discussion, Beltian bodies are not found on acacia species that lack a relationship with ants in the genus *Pseudomyrmex*.

Foliar nectaries. The foliar nectaries are nectar-producing glands on the dorsal side of the petiole and/or rachis of all leaves of mature shoots (Fig. 1b). They are elevated trough-shaped and 0.5-6 mm in length. Large nectaries produce a sphere of clear, sticky nectar about 2 mm in diameter during a 24 hour period; the nectar flow is heaviest about one hour before sunrise. The workers of *P. ferruginea* collect the nectar as it appears; if the shoot is unoccupied, many species of Hymenoptera visit the nectaries. A shoot 2 m tall with 200 leaves produces about 1 cc of nectar during a 24 hour period. The nectar consists of about equal parts by weight of sucrose and fructose at an approximate concentration of 40 mg/cc H_2O (determined in the laboratory of Dr. H. T. Gordon, University of California, Berkeley). While the foliar nectaries are mentioned casually in almost all accounts of the swollen-thorn acacias, no detailed accounts of their morphology or physiology are published.

Stipules. Over 99 percent of the bilaterally symetrical stipules of *A. cornigera* can be placed in two size classes: minute and swollen. Minute stipules are 3-8 mm in length, and hard and needle-tipped when dry. They accompany about 50 percent of the leaves produced by a shoot during its lifetime and are for the most part confined to the leaves in axillary leaf tufts and on flowering branches. The ants do not enter them. Mature swollen thorns (Fig. 2 and 19) are 2-25 cm in length, hard-walled, and hollow with sharp tips when dry. The "V" shaped type A thorns are part of the large leaves found on lateral branches and the main vertical axis of the shoot. The highly convoluted type B thorns are found on short branches originating in the axils of type A thorns; though fewer in number, the type B thorns have 1-2 cc of space in each of them and thus constitute the major source of space that the colony has for rearing brood (Fig. 20). The volume of space available to the colony in a 3 m tall shoot is about 400 cc. Completely dry thorns that have not been cleaned out by *P. ferruginea* are about one-fourth empty, but are not available to the ants because they cannot cut into the dry thorn.

The walls of swollen thorns have a number of characteristics which are of importance to the ants living within them. By two weeks of age, a swollen thorn is usually completely dead and dry except for a narrow median ventral strip of living vascular tissue connecting the leaf petiole with the branch. The hard and polished outer surface does not readily absorb water but the inner walls are quite absorbent. The walls are 0.7-4 mm thick and in general the type B thorns have the thickest walls. Type B thorns often have a raised ridge of hard tissue running along an inside ventral surface;

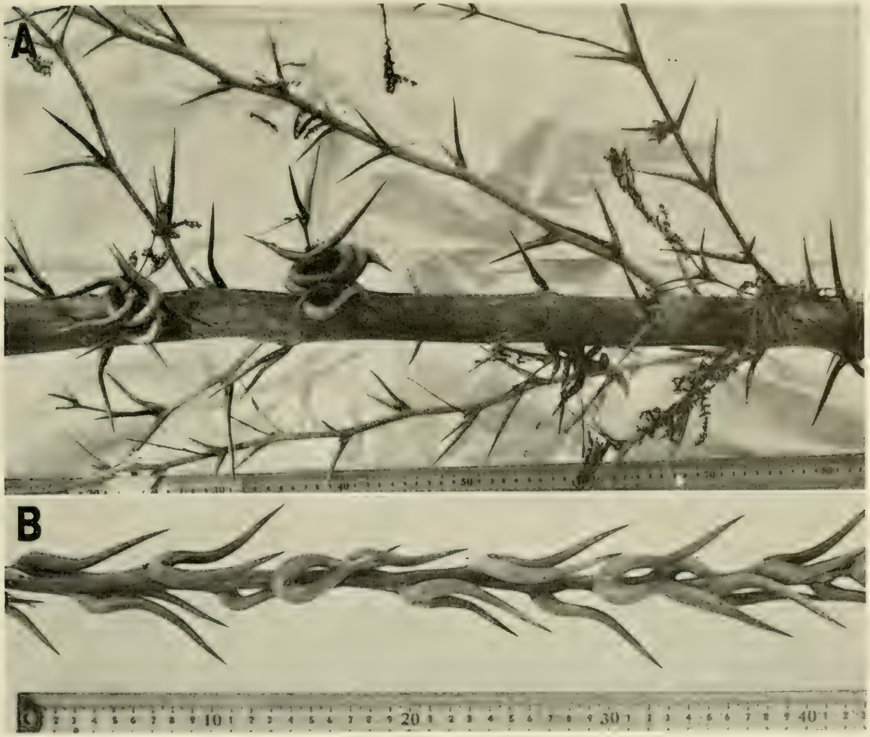


FIG. 19. a. A 75 cm long section taken from a point one-half way up a 4 m tall occupied shoot of *Acacia cornigera* that was cut a week before the photograph. The type B thorns form tight clusters surrounding each short axillary branch that bears them, while the type A thorns are borne on the elongate lateral branches. This shoot was about 24 months old and growing in dense, ungrazed regeneration along the Rio Tonto, 8 km east of Temascal. b. A 45 cm long section taken from the terminal 150 cm of the main axis of the shoot in Fig. 19a. This portion of the shoot characteristically bends over at the end of the rainy season and the next year's main vertically lengthening axis develops from a thorn axil near the base of this portion of the shoot.

this may serve as a reinforcement. They are extremely tough and hard to split by hand; they do not break across the grain but split along the longitudinal axis. Type A thorns are more brittle and break across the grain. Both types are most easily opened by cutting through the living tissue at the thorn base.

The walls of the thorns have a noticeable effect on the microclimate inside the thorn. Temperature recordings made with thermistor probes (Yellow Springs Instrument Co. #402 probe) show that 1) fully insolated dark thorns can be as much as 2.5° C. hotter inside than light colored ones, 2) at high air temperatures outside when the air temperature is rising or falling, the temperature inside the thorn rarely lags more than an hour behind that outside the thorn, and 3) at low temperatures, the temperature

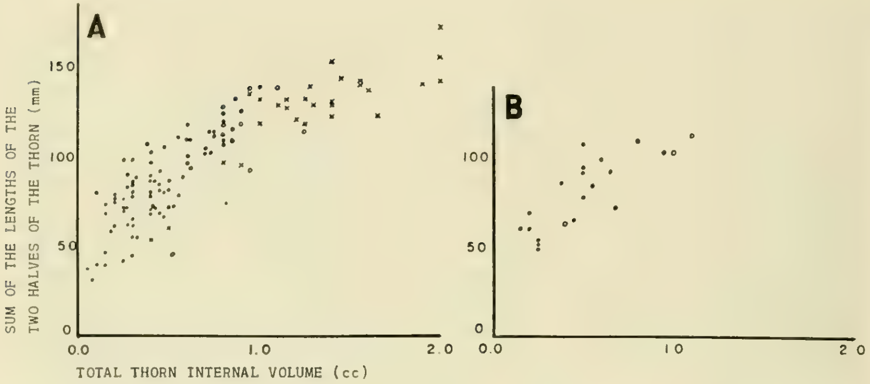


Fig. 20. a. Graph of the relation between thorn volume (abscissa) and the sum of the lengths of the two sides of the thorn (ordinate). Type A thorns are represented by dots, type AB thorns by circles, and type B thorns by x's. This graph contains all of the swollen thorns that had been hollowed out by *Pseudomyrmex ferruginea* on the queen-shoot in Fig. 11. The one small type AB thorn and the two small type B thorns had only one-half of the thorn swollen. b. Graph of the thorns on the auxiliary-shoot in Fig. 11.

inside the thorn is rarely more than one-half degree C. higher than the air temperature even when the thorn is fully insolated. While the absorbent inner thorn wall probably soaks up any excess fluids from the ants in the thorn, the outer thorn wall probably serves as an effective barrier against water loss during the dry season, and prevents the thorn contents from being drowned during the rainy season. The entrance hole of the thorn is usually plugged by an ant's head, making the thorn an almost watertight container.

The rate of swollen thorn production varies greatly in respect to the time of year and the size of the shoot. Since only about one-half of the leaves produced have swollen thorns, it is normally only when new branches are produced that the number of swollen thorns on a shoot increases. A shoot occupied by *P. ferruginea* produces about 200 swollen thorns during its second year of growth (changing from 2 to 3.5 m in height). These thorns would weigh at least 600 g. In five years of growth a shoot produces on the order of 4 kg of thorns.

Development of vegetative features. In repeatedly disturbed areas such as pastures, crop fields, and roadsides, the majority of *Acacia cornigera* shoots grow from root stocks older than their respective shoots. In natural disturbance sites, the shoot is more often of the same age as the root stock. It appears that most root stocks of *A. cornigera* die after succession has proceeded without interruption (no grazing, burning or cutting) for 10 to 20 years. Therefore the shoots are usually of the same age as their roots following the first clearing of an old forest. In this case, the regeneration of *A. cornigera* is by seed. The shoots under experimental observation in this study were nearly all younger than their roots because the study sites had been repeatedly cleared during the past 30 years. *A. cornigera* shoots derived directly from seed are very difficult to find except during the first two months of the rainy season. Once a seedling growing in full sunlight has reached a height of 75 to 100 cm, it is difficult to distinguish it from a new sucker growing from a 2-3 year old root system unless the upper part of the root stock is exposed and examined. Large older roots produce new suckers that are very mature in appearance.

Very young seedlings do not initially possess the diagnostic characteristics of a swollen-thorn acacia: swollen-thorns, Beltian bodies, and foliar nectaries. The number of pinnae and pinnules per leaf increases gradually until the 10th to 20th leaf. One or two Beltian bodies appear on the basal pinnules of the basal pinnae of the 7th to 16th leaf. Each successive leaf bears a few more Beltian bodies, both further out on the leaf and further out on the pinna. The first type A swollen thorn is produced at the 9th to 12th node. The first axillary branch with a type B thorn does not appear until the shoot has 75 to 100 nodes. The first traces of a foliar nectary do not appear until the 5th to 8th leaf and the first large functional nectary is usually on the petiole of the leaf associated with the first swollen thorn. Multiple nectaries on the leaves appear at about the same time as the first type B thorns. On well-watered soil in full sunlight, it takes a seedling 30 to 45 days to produce its first swollen thorn. It should be noted that while Beltian bodies and foliar nectaries are not present on the newly germinated seedling, they are present by the time the first swollen thorn is produced and therefore a new founding queen in the first swollen thorn has an immediate source of food.

Shading suppresses the development of Beltian bodies, nectaries, and swollen thorns. A heavily shaded seedling, by the time it produces its 40th leaf, is still producing thorns, Beltian bodies, and nectaries with the same form and size as those in the 10th to 20th nodes of fully insolated shoots (Fig. 21). Under the climatic regime at Temascal, a fully insolated seedling on well-watered black soil will grow at least 200 cm in a year. However, since seedlings are often not occupied by an effectively protective colony of *P. ferruginea* during their first year of growth, they receive moderate to severe damage to the shoot tips by phytophagous insects and thus rarely grow more than 100 cm in the first year.

Suckers from cut or burned stumps have much more the appearance of mature shoots than do seedlings. The leaves on a new sucker from a large stump often have a Beltian body on the end of every leaf segment, large type A thorns and a few type B thorns, and well developed foliar nectaries. The immediate production of these properties by the acacia are of obvious importance to a large ant colony moving from a shoot that has been cut into the new sucker growing from the shoot's stump.

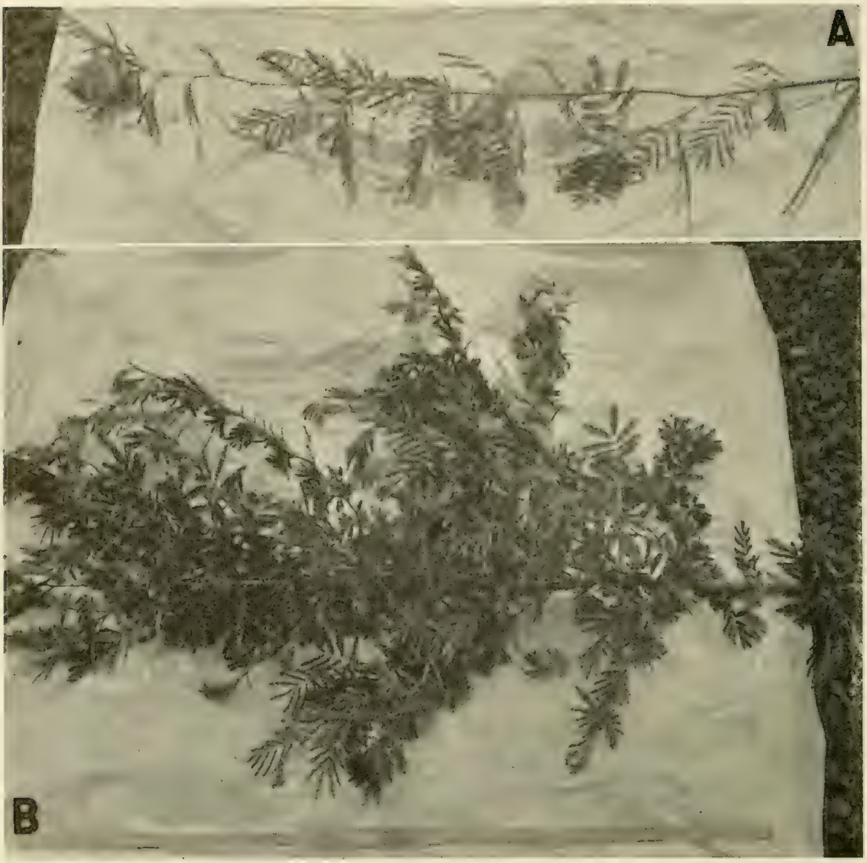


FIG. 21. a. An occupied shoot of *Acacia cornigera* that had grown for 7 months from a cut stump in the dense shade in plot R. Photo 17 Mar. 1964. b. An occupied shoot of *Acacia cornigera* that had grown for 7 months from a cut stump in the open brushy pasture adjacent to plot F. Photo 17 Mar. 1964. Both shoots were growing on the same kind of soil and are representative of the differences found between shaded and insolated shoots. The shoot in Fig. 21a had about 150 workers in the ant colony while that in Fig. 21b had about 2,000 workers; both were colonies that had invaded from other shoots that had been cut. Both photographs to same scale.

The growth rate of occupied sucker shoots is noticeably higher than that of occupied seedlings. It is commonplace for a sucker from a large stump to grow 400 cm upward in a year. Sucker regeneration takes place at any time during the year, but as the sucker ages it becomes more responsive to seasonal climatic changes (leaf drop during the dry season, not initiating growth until the first rains). In evaluating height increments for shoots of various ages, the time of year during which the growth took place must be considered.

REPRODUCTIVE BIOLOGY. *Pollination. Acacia cornigera* is pollinated by a number of species of bees (e.g., *Bombus medius, Ceratina extimia,* Megachilidae, Halictidae). These bees are occasionally chased by *Pseudomyrmex ferruginea,* but the workers are not effective in keeping bees off the flowers. While the workers of *P. ferruginea* are commonly seen digging into the pollen covered surface of the inflorescence, it is doubtful that they effect pollination by carrying pollen from one flower to another since they are constantly cleaning themselves. The major flowering period varies widely from one part of the study area to another, but is usually within the period from the middle of the dry season to the first month of the rainy season. The buds of the flower bearing branches are first evident about three months before flowering begins. Small green legumes are present shortly after flowering, but these require 10 to 12 months to mature. This means that the acacia must live this long after flowering to produce viable seed.

Seed production. A. cornigera produces comparatively few seeds for a plant of disturbed sites. In its lifetime, a shoot produces about 60,000 seeds. Better than 99 percent of these seeds are destroyed by the larvae of bruchid beetles. In the Temascal area, the common species were *Acanthoscelides oblongoguttatus* Fahr., *Mimosestes* sp., and *Stator subaeneus* Schaeffer. The adults of these beetles may be found on mature pods at any time during the year, and the author has yet to find a mature seed pod of *A. cornigera* that was over two months old and not attacked by one of these species of bruchids. Some natural enemies of the bruchids have been discovered, but an investigation of their biology has not been made. When a seed crop was picked before bruchid exit holes were evident in them, as many as 75 percent of the seeds were undamaged. However, when the first generation of beetles emerges, the beetles oviposit in those legumes which are not infested and complete the seed destruction. The legumes may remain on the tree for two to five months after maturation.

That some of the seeds escape destruction is due to one of the two methods of seed dispersal used by *A. cornigera:* birds and water. Birds readily split the pods to eat the sweet yellow pulp around the seeds and in doing so ingest some seeds. In the Temascal area, the commonest species are the Black-headed Saltator *(Saltator atriceps),* Grayish Saltator *(Saltator coerulescens),* and the Plain-tailed Brown Jay *(Psilorhinus mexicanus).* The seeds that are distributed by defecation normally fall in relatively good sites for germination since these four birds are common in new second growth vegetation. Secondly, when seeds are removed early from the site of bruchid infestation, some escape damage. They are eaten shortly after the pods ripen, as food for these birds is normally scarce during the dry season. Seeds taken from the intestines of these birds germinated normally.

A second group of birds open the pods but do not eat the seeds (Black-throated Oriole, *Icterus gularis,* Derby Flycatcher, *Pitangus sulphuratus,* and the Melodious Blackbird, *Dives dives*). They eat the yellow pulp around the large seeds, but let the seeds fall to the ground where they sometimes germinate directly under the parent tree. By opening the pods they likewise remove some seeds from the site of bruchid infestation. The workers of *P. ferruginea* are often consumed in large numbers by the Black-throated Oriole but rarely found in the other species mentioned.

Throughout much of the study area, there are two general forms of legumes; one has a very thin wall that splits by twisting when dry, and the other has a thick wall that does not split. There are intermediates. The birds appear to find the thin walled form much easier to open; many more of these are opened than the thick walled form. Associated with this, it is the thin walled form which has spread away from the natural disturbance sites along watercourses in areas newly opened to agriculture. If not opened by birds, the thin walled form eventually twists open and drops its seeds; by this time the bruchids have destroyed better than 99 percent of the seed. The thick walled form appears very well suited to dispersal by water. In old established pastures, the thick walled form is generally the dominant form.

Invasion of new sites. Land recently exposed to plant colonization (landslides, sand bars in rivers, lake beaches, river banks) and newly cleared forest (over 10 to 20 years old) is very slowly colonized by *A. cornigera* in the area between Temascal and La Granja. Despite the nearby presence of seed bearing shoots, the invasion rate rarely exceeds ten established plants per acre per year and is usually much lower. This appears to be most directly associated with the high mortality rate of unoccupied seedlings. However, most of the man-made disturbance sites are repeatedly cleared of their aboveground vegetation by fire or cutting. Roots and seeds of *A. cornigera* are often not destroyed by this clearing procedure. As the seed invasion continues, and the shoots already present drop seed around their bases, the density of root systems increases to levels as high as 2,000 per acre (estimate from swamp pasture east of Tuxtepec, Oaxaca, Mexico) and 800 per acre (counts from dry pasture in plots N and O). Brushy pastures, with their occasional burning and/or clearing (2-5 year intervals), and vegetation cover opened by browsing, have the optimal conditions for producing large populations of *A. cornigera.*

Not all root stocks bear maturing shoots. During any one regeneration cycle, 10-75 percent of the root systems have a vigorously rising shoot occupied by *P. ferruginea.* The remainder have short shoots that are usually less than 75 cm tall with 4-20 swollen thorns. Of these thorns, 10-100 percent have founding queens of *P. ferruginea* in them. As a colony develops in situ, or the shoot becomes an auxiliary shoot, a rapidly rising sucker develops if not heavily shaded.

Under well developed canopies that are young enough still to have mature *A. cornigera* in them, there is a new crop of *A. cornigera* seedlings during the first two months of the rainy season. During the following three years, this cohort suffers nearly 100 percent mortality; individuals rarely grow over 1 m tall and are poorly developed (Fig. 21a), even when occupied by an established colony of *P. ferruginea.* On these shaded shoots, there is a very low rate of production of new colonies in situ. While ample founding queens are present, some factor in the shaded site often prevents successful colony growth. This is very likely associated with the low rate of nectar and Beltian body production.

REQUIREMENTS IN THE PHYSICAL ENVIRONMENT. Following Holdridge's classification (1964), *Acacia cornigera* is found in the study area from Tropical Tropical Arid Forest to Low Subtropical Dry Forest to Low Subtropical Wet Forest to Tropical Tropical Moist Forest. Following Leopold (1962), it is found in Pine-Oak Forest, Mesquite-Grassland, Rain Forest, Tropical Evergreen Forest, and Savanna. Despite this occurrence in a wide range of formation types and vegetation life zones, there are several common denominators to its habitats: 1) they are disturbed sites where sunlight reaches very close to ground level, 2) since such sites are frequently cleared of all vegetation above ground, the regenerating occupied suckers of *A. cornigera* are able to initiate growth as canopy members or emergents, 3) being fully exposed to sunlight, the canopies of *A. cornigera* experience the highest air temperatures that can be achieved by the prevailing weather, 4) the other species present as canopy members during the early stages of succession have rapid growth as well, 5) there are high populations of phytophagous insects present and these sites are frequently subjected to cattle grazing and browsing, and 6) the moisture content of the soil fluctuates greatly, depending on the season.

Within a wide range of temperature, rainfall, and soil type regimes, the presence and density of *A. cornigera* is primarily a function of the disturbance history of the plant community. In the literature, it is characterized as a plant of the land-ward side of ocean dunes to upland foothill oak forest (1,200 m) associated with pasture and frequently cleared areas (Skwarra, 1934a, 1934b; in the state of Veracruz); as a plant of the tropical littoral to 400 m elevation in clearings, open country, and roadsides (Wheeler, 1913; in Guatemala and Costa Rica); and as a plant of ravines, riverbanks, savannas, and other naturally disturbed areas (Belt, 1874; near Matagalpa, Nicaragua). It appears that Wheeler's discussion of *A. cornigera* in Costa Rica applies to *Acacia collinsii* Saff. since *A. cornigera* (=*Acacia nicoyensis* Schenck) has not been found at Alajuela or other sites over 200 m elevation during intensive searches for this plant in Costa Rica. In all cases *A. cornigera* is regarded as a plant of lowland, tropical, disturbed plant communities.

At the margins of its range, the general density of shoots is often very low, there being only an occasional streamside, roadside or pasture plant. Yet within 10-15 km or less of this margin, there are often very dense populations in swamps, pastures or roadside ditches. If a site at the margin of the range is suitable for the growth of one shoot, the population often builds up to densities equal to those found in the most central parts of the range.

Moisture. Within the study area *A. cornigera* is more restricted in respect to aridity than is *P. ferruginea.* This is evident from Figure 6 where it can be seen that *P. ferruginea* crosses the interface between the ranges of *A. cornigera* and *A. sphaerocephala* at 11 mi. N.E. Ciudad Valles, 27.5 mi. S. Panuco, 22.8 mi. W. Conejos, and between Veracruz and Anton Lazardo without interruption. At each of these sites, the climate becomes drier as one moves into the range of *A. sphaerocephala.* At the range limits of the distribution of *A. cornigera* to the north, northwest, and northeast, and at the break at 28.8 mi. W. Conejos and 10 mi. S.E. Conejos, its disappearance appears to be in agreement with regions of about 1,000 mm annual rainfall and a dry season of about 6 months duration. Except at 20 mi. N.W. Ciudad El Maiz, it is replaced by *A. sphaerocephala* at these points. At this place, the last plants of *A. cornigera* are found in barren rocky pastures with *Opuntia* spp. and *Acacia farnesiana.* These sites appear to have been covered with oak forests at one time. *A. sphaerocephala* may be prevented from reaching this area by a band of east facing slopes of the Sierra Madre Oriental in the area of Ciudad El Maiz with higher rainfall (approximately 2,000 mm annual). There is a strong possibility that the inability of *A. cornigera* to extend its range into drier sites is associated with its inability to hold its leaves and produce new axillary leaf tufts when the dry season is too long. If the shoot is completely leafless for more than a month, the ant colony dies or has its numbers greatly reduced by starvation. If this happens, the acacia enters the rainy season in an essentially unoccupied condition with consequent poor growth. *A. sphaerocephala* can hold some leaves and produce new leaves at least a month longer than can *A. cornigera.*

In the area to the south of the city of Veracruz along the beach above Anton Lazardo, *A. cornigera* is replaced by *A. sphaerocephala* on the dunes within 500-3000 m from the high tide line. At Tuxpam, Tecolutla, and Coatzocoalcos, *A. cornigera* has been found as an occasional plant within 50 m of high tide, being in some cases the first woody plant. Veracruz has a longer dry season than either of the three later sites, and it appears that the relatively well drained new dunes are too dry for *A. cornigera.* The *A. sphaerocephala* on these sites forms a low dense mat which is not occupied by *P. ferruginea.*

There are also inland sites within the range of *A. cornigera* that are apparently too dry for it. In the dry hilly oak forest around Villa Azueta, the acacia is virtually absent even on the roadsides; only 2-5 km away in the wet river bottoms it is very common. Along the road southeast of Conejos the first appearance of *A. cornigera* is in roadside swamps as the altitude decreases moving down the arid shelf from the west. In the Temascal area, the oak-grass covered knolls often have no *A. cornigera* on them. This may in part be due to the rapid rainfall runoff through laterite soils although the high frequency of fires is probably of greater importance.

Temperature. At 6 mi. S.W. Tamazunchale, 8 mi. S.W. Martinez de la Torre, 28.5 mi. W. Conejos, and Valle Nacional, the failure of *A. cornigera* to extend its range appears to be associated with lower temperatures. At each of these sites, the number of days with the maximum temperature below 24° C. is about 90-110 per year. During weather of this frigidity, the workers of *P. ferruginea* are generally not active outside of the thorns. One result of this is that the colony is reduced in size, apparently through starvation. During the cold period at Temascal in December through February, almost no vertical growth occurred in experimental plots. Even those plants with intact shoot tips had almost no growth. Shoot tips are rapidly removed by phytophagous insects during cool weather owing to the lack of patrolling workers of *P. ferruginea*; these shoot tips are only very slowly replaced by the acacia during cool weather. *A. cornigera* is apparently cold-hardy as is shown by experience with cultivated and escaped shoots in Florida. They are not damaged by occasional frosts and survive the coldest winters. Fire rather than cold seems to be the factor which prevents naturalization (C. F. Dowling, personal communication).

Soil type. High densities of *Acacia cornigera* have been found on beach sand, red and yellow laterites, black soil over limestone, black swamp soils laden with high organic matter, and on many other unidentified soil types. Within the study area and its range, no soil types have been found on which *A. cornigera* is consistently lacking. The low densities commonly recorded on red-yellow laterite hills are largely due to the disturbance history (regular burning) rather than unsuitability of the soil. Once these areas are farmed sporadically and/or grazed, *A. cornigera* sometimes becomes common on well watered laterites.

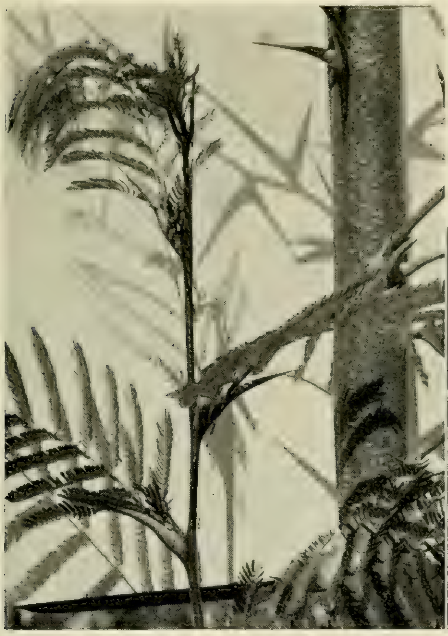
Sunlight. As is the case with many plants of early succession, *A. cornigera* requires direct or intense indirect sunlight for normal development of swollen thorns, Beltian bodies, flowers, and height. Most of the occupied shoots in the study area are canopy members or emergents, or growing in open communities lacking surrounding vegetation. If the acacias were able to grow well in shade, the interrelationship with the ant would lose much of its significance inasmuch as the single most important role of the colony of *P. ferruginea* is to prevent damage to the shoot tips, which, in their growth, keep the shoot canopy in the sunlight.

The major portion of *A. cornigera* shoots growing in heavy shade can be placed in one of two size classes. Most frequently, they are 5-100 cm tall with few mature leaves, few swollen thorns, and no intact shoot tip. The thorns are often partially rotted and many leaves have only minute stipules. While founding queens are sometimes found in the thorns, more often they are empty and only very rarely are such shoots occupied. In the other size class are placed the rare slender vertical shoots of 100-250 cm height. They have small swollen thorns and internodes one and one-half to three times the normal length (Fig. 21a). The number of Beltian bodies per leaf is reduced and they are pale in color. The foliar nectaries are small with a reduced nectar flow. These slender shaded shoots are usually occupied by *P. ferruginea*, associated with small gaps in the canopy and developed from old root stock of senescent emergents. Most shoots in both size classes do not reach the canopy or flower; they usually disappear within three years. If they do reach the canopy, they develop normally.

The height of the canopy has some effect on the survival of shaded shoots. Where the canopy is very low (e.g., 120 cm following six months of regeneration after cutting or burning), shoots in the smaller size class occasionally have a burst of growth during the dry season which carries them into or above the canopy. This is apparently due to the nearly full sunlight that they receive due to the leafless nature of the general canopy. This circumstance is often associated with the invasion of the shoot by a large colony of *P. ferruginea*. Shoots in the taller size class are usually old enough so that they respond to the dry season by reduced vertical growth rates and partial leaf drop.

Fire. The shoot of *A. cornigera* is easily killed by fire. Light ground-level fires are common during the dry season throughout the study area. The heat is often of sufficient intensity to kill the branches and leaves of shoots 3-6 m tall. Shorter shoots are often consumed entirely. If the fire only scorches the bark at ground level, the shoot is killed but the ant colony survives to occupy the new sucker shoots (Fig. 22, 23). The pruning activities of *P. ferruginea* in the immediate area of the shoot during the rainy season (Fig. 35) lower the quantity of dry litter present around the base of the shoot and thus are partly responsible when the fire is not hot enough to kill the ant colony (and even in some cases, to kill the shoot).

The root stock does not appear to be damaged by fires. However, in areas where fires occur every year (oak-grasslands, canefields, some pastures and milpas), *A. cornigera* is usually not present 2-4 years after the first burning. This is because the regular fires destroy all of the mature colonies of *P. ferruginea* and the new sucker shoots are unoccupied. This system is described in greater detail in Janzen 1967b.



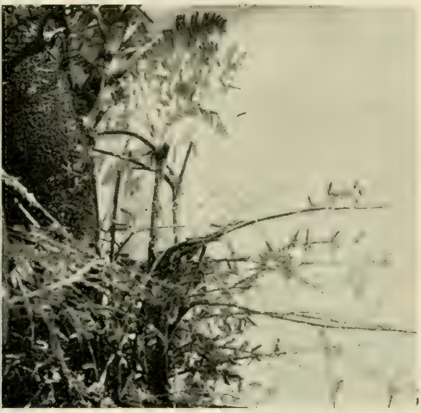


FIG. 22 (left). An occupied sucker shoot from the base of a fire-killed shoot. The parent shoot was 4 m tall and the sucker shoot 122 cm tall. Only the terminal 25 cm of the shoot is shown. There are 12 workers of *Pseudomyrmex ferruginea* in the photograph. The entire colony will eventually move from the dead shoot into the new shoot as it grows. Photo 11 Jul. 1964.

FIG. 23 (right). Unoccupied sucker from the base of a fire-killed shoot. The parent shoot was 4 m tall and the biggest sucker 15 cm tall. The upper 13 cm of the shoot is shown in the photograph. This shoot was about 15 m from the shoot in Fig. 22. Sawdust from wood-boring beetles in the dead shoot can be seen on the leaves, and the branches of the living shoot have been damaged by *Coxina hadenoids* and other insects. Photo 11 Jul. 1964.

POPULATION GROWTH PARAMETERS. *Height increment.* The height of a shoot of *Acacia cornigera* must be considered in relation to the surrounding vegetation and the ant colony occupying the shoot. In the course of this study, comparisons of height increment between occupied and unoccupied shoots have provided reliable indications of the efficiency of the ant colony in keeping phytophagous insects off the shoots. However, changes in mean and individual heights must be evaluated in respect to the type of shoots (seedlings or suckers), age of shoots, time of year, height and density of surrounding vegetation, and percentage of the shoots occupied by *Pseudomyrmex ferruginea.*

Even when occupied by a large, established colony of *P. ferruginea,* a seedling in its first and second year of undisturbed growth usually does not produce a shoot of more than one quarter the weight and size of the sucker that can be produced in one year by a four year old root system with a 4 cm diameter stump. Seedlings and suckers do not become leafless during the dry season of their first year of growth. Intact shoot tips cease vertical growth only during the cool dry period. However, the seedling with its relatively shallow root system (less than 1 m) is often not capable of replacing a damaged shoot tip during the dry season. The dry season only slows the replacement of shoot tips on suckers from large stumps, and thus height increment continues.

Even though occupied by a large colony of *P. ferruginea,* shoots over a year old usually cease vertical growth sometime between November and February. The cessation is associated with a failure to replace shoot tips eaten by defoliating insects rather than to dormancy of intact shoot tips. This period is both cool and dry, and most new growth is in the form of axillary tufts and leaves. The older the shoot, the longer after the first heavy rains before a positive height increment occurs. Shoots in the 1-2 year age class are variable; many show large increases in height within a month before or after the first rains. Shoots over two years old often do not initiate vertical growth until weeks or even a month after the first rains. In addition, the main vertical branch usually starts a meter or more below the top of the shoot. It is therefore often as long as a month after the rains begin before any substantial change in height occurs. This type of growth pattern is repeated each year while the shoot maintains its position in the rising general canopy. It is clear that comparisons of height increments at different times in the year must be identified with the time of year involved.

In almost all plant communities where *A. cornigera* has an even or increasing population density, occupied shoots are canopy members or emergents (Fig. 10-14, 24). In secondary succession under three years of age, in which the vegetative cover is for the most part fromed by regeneration from cut stumps, the tallest plants are *A. cornigera* and the plant population with the greatest mean height is that of *A. cornigera* occupied by *P. ferruginea.* Apparently associated with the need to maintain such a position in the general vegetation canopy, partially shaded shoots grow very strongly vertically while fully insolated shoots develop in a lateral direction as well.

A. cornigera has one of the largest height increment rates of the woody plants in early secondary succession in the study area. On 10 July 1964, the height and condition of 20 regenerating sucker shoots with 1-2 year old colonies of *P. ferruginea* were recorded. These were emergents from a canopy of herbs and shrubs 60-100 cm high that were occasionally browsed by cattle. The acacias were chosen to be between 100 and 200 cm tall with no evidence of present or previous insect damage to the uppermost six nodes. For 18 days these plants were examined every third day and each plant with a damaged shoot tip was rejected from the sample. On 28 July, nine shoots remained. These shoots had an original mean height of 148 cm (s.d.=26

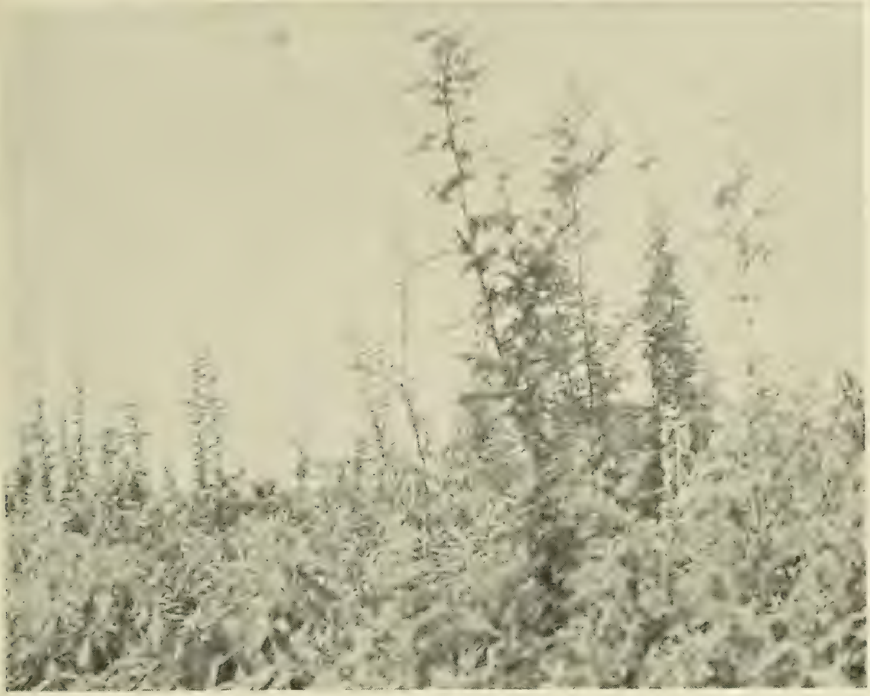


FIG. 24. Emergent occupied shoots of *Acacia cornigera* in subplot O-2. These year old sucker shoots were 150-300 cm in height and grew from stumps cut in June 1963. At least the upper 100 cm of each shoot seen in the picture had grown since the first heavy rain on 20 May 1964. There are many unoccupied shoots of *A. cornigera* below the general vegetation with its canopy at about 100 cm height. Photo 1 Aug. 1964.

cm) and final mean height of 193 cm s.d.=38 cm). The mean of the height increments was 45 cm (s.d.=11 cm). This represents a mean height increment of 2.50 cm per 24 hours by shoots which received on damage to the shoot tip for 18 days well into the rainy season. At the Temascal weather station, the mean maximum temperature for this period (10-28 July) was 30.4° C., and the mean minimum was 22.3° C. Precipitation was 284.8 mm. It is believed that this rate of growth during the rainy season is representative of undamaged shoot tips of lengthening branches on seedlings over one year old and sucker regeneration of all ages. It is representative of the rates of height increment in the absence of shoot tip damage. Once the acacia shoot is part of, or emergent to, a gradually rising general canopy over 3-4 m in height, the representative height increment of occupied shoots is 1-2 m per year (this figure includes shoots receiving various amounts of insect damage).

Age-class representation. The proportions of different aged trees in natural vs. man-made disturbance sites are often quite different. In natural disturbance sites, it is common to find acacias of all ages and the only large size class is that of new seedlings near the bases of seed bearing trees during the rainy season. This type of age-class distribution is generally associated with the more irregular disturbance history of natural sites. In man-made disturbance sites that lack heavy cattle browsing, it is common for all occupied shoots to constitute one size class and the unoccupied another. All the shoots are nearly the same age due to the total destruction of the vegetation often wrought by fire or cutting. The occupied shoots are canopy members or emergents, and the unoccupied shoots are under the general canopy of the plant community. This difference between the two groups is accentuated as the unoccupied shoots are stunted and eventually removed by biotic mortality agents. With increasing grazing pressure and the subsequent opening of the plant community, the distinctiveness of these two size classes is reduced because unoccupied shoots in full sunlight sometimes live long enough to become occupied and then grow to maturity.

Mortality factors. Mortality of the above-ground shoot, and mortality of the root system are two quite different parameters. In general, death of the root system requires several successive destructions of the shoot, or else 6-18 months of repeated destruction of the new shoot tips. The amount of stress tolerated by a root system appears to be directly related to the size of the root system, and the size of the shoot that was destroyed. When uninterrupted shoot development is allowed for periods of two or more years between shoot destructions, an individual root system lives at least 30 years and probably much longer. If suckers from cut stumps are heavily shaded, the root system finally dies. However, when plant communities that are 10-15 years old are cleared, old and apparently dead *A. cornigera* stumps sometimes produce small shoots which grow into completely developed mature plants if they become occupied by *P. ferruginea.* In natural disturbance sites such as river banks and arroyos, entire root systems are often washed out. These plants occasionally root where they are deposited by the receding waters.

In the Temascal area, biotic mortality agents of roots are almost never observed. In one case, a localized aggregation of pocket gophers *(Heterogeomys hispidus)* killed about one-half of the *A. cornigera* in two half-acre areas by uprooting them and eating the roots (73 plants). This damage occurred during the dry season and stopped when the rainy season began.

In the Temascal area, there are various agents that destroy the entire shoot *of A. cornigera* but leave the root system undamaged. When clearing roadsides or around houses, the shoots were often cut along with the other vegetation. While *A. cornigera* is occasionally left standing out of fear for the ants, quite often it is singled out and cut because the people do not care for the ants. Newly cleared cornfields, pastures and roadsides are often burned if cut in the dry season. Since the entire shoot is lying at ground level, the ant colonies are destroyed by these fires. Many acres of unused land are burned by fires that escape from set fires. Since the shoots in these areas are upright, the intensity of the fire regulates whether the trunk is just scorched (killing the shoot but not the ants) or the entire shoot is consumed. Many sites go for 2-3 years without accidental fires and then may be burned each of 1-3 successive years. This random destruction of *A. cornigera* has much less total impact on the acacia and ant population than does the deliberate annual burning of some lands for agricultural purposes (e.g., sugar cane fields). In this case, the roots of *A. cornigera* are systematically deprived of their shoots and eventually disappear from the site.

The most important biotic remover of entire shoots in the Temascal area is the cricetid rodent *Sigmodon hispidus* (hispid cotton rat). It eats *A. cornigera* most frequently during the last two months of the dry season; at this time *A. cornigera* is one of the few shrub-sized plants that has green foliage and tender stems. It cuts unoccupied shaded shoots, under partially to entirely closed canopies 50 to 150 cm high. These shoots are usually 10 to 100 cm tall. The bark and supple branches are eaten. Usually the only evidence of the rat's feeding is a 2-10 cm tall stump, a pile of wilted leaves, loose thorns, wood shreds, and light brown oval fecal pellets. *S. hispidus* also climbs to the top of emergent unoccupied shoots to cut off shoot tips. It is extremely common in 50-200 cm high regeneration in pastures and fallow cornfields. During the last month of the dry season, it may remove as much as 75 percent of the unoccupied shoots below these low canopies. *S. hispidus* is attacked by *P. ferruginea* when it attempts to cut an occupied shoot and notches are occasionally found in the trunks of occupied shoots.

There are only a few insects which kill entire woody shoots, and only one of these is numerically important. The larva of the buprestid beetle *Chrysobothris* sp., near *C. multistigmosa* Manh. occasionally kills 2-3 m shoots by girdling the trunk from the inside. This beetle is very common and is very often responsible for the death of unoccupied stumps during the first six months of sucker regeneration. The female beetles are usually deterred from ovipositing in the newly cut stump by the ants. When preparing oviposition sites, the rare cerambycid beetle *Onicideres poecila* Bates cuts off unoccupied shoots of *A. cornigera* that are 60-120 cm tall (Fig. 25). The cut is made 20-40 cm above the ground and the female oviposits in the cut shoot. A closely related cerambycid, *Lochmaeocles cornuticeps* is common in the Campo Cotaxtla area. Adults of this species completely girdle the trunks of unoccupied shoots up to 4 m tall and oviposit in the dead shoot.

There is very high mortality of very young seedlings. While apparently very resistant to fungus attack, seedlings are readily eaten by insects. Moth larvae (Noctuidae, Arctiidae) and orthoptera do the most damage. When

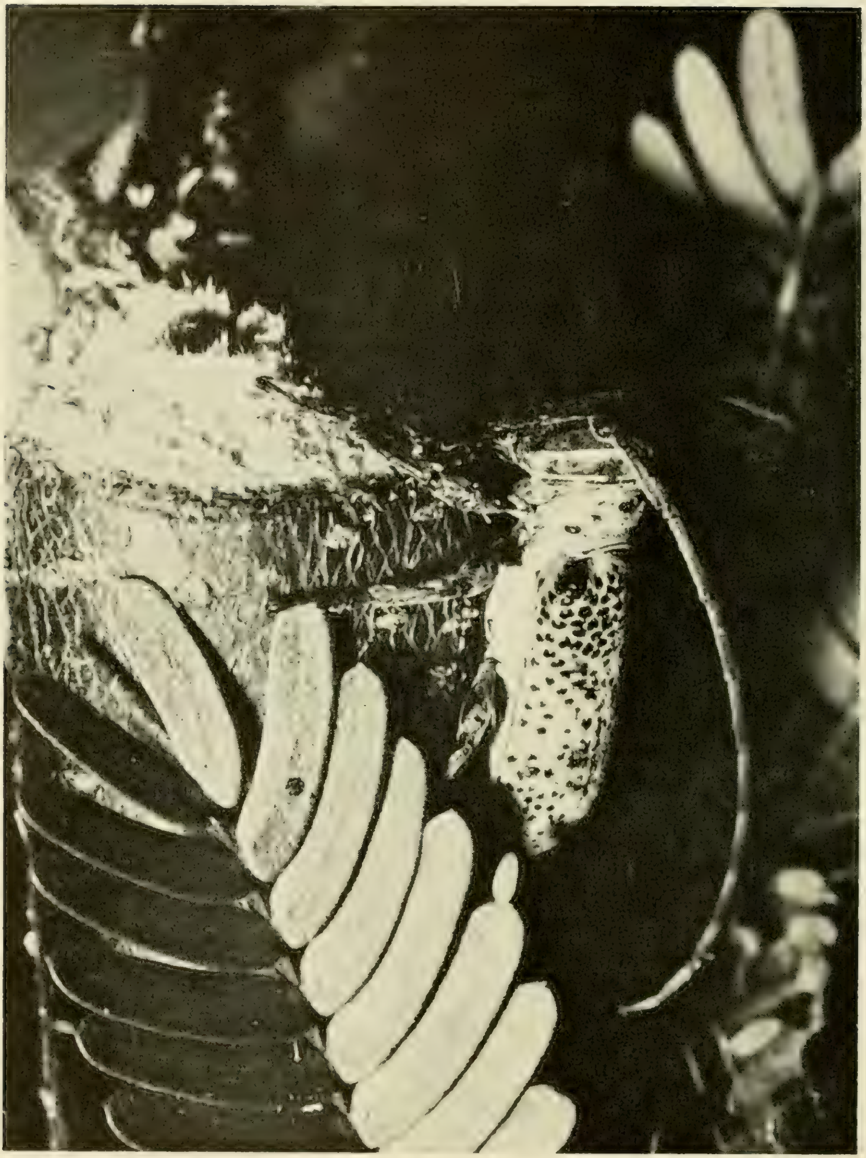


FIG. 25. An adult female of the cerambycid *Oncideres poecila* immediately after cutting an unoccupied shoot of *Acacia cornigera* in subplot N-2. The shoot was 12 mm in diameter. She oviposited in the portion of the shoot that fell to the ground. The cut shoot had an auxiliary-unit of *Pseudomyrmex ferruginea* living in the thorns but there were no workers active outside of the thorns owing to cold weather. Photo 11 Jan. 1964.

the leaves are removed from very young seedlings, the entire plant dies. In addition to insects, black rats *(Rattus rattus)* and lizards (Iguanidae) on occasion eat very young seedlings of *A. cornigera.*

Damaging factors. With the exception of the activities of man and damage by *Sigmodon hispidus,* biotic mortality agents are rarely observed in sign or action. However, damage to *A. cornigera* is very commonly encountered. Most of the insects responsible for this damage in the Temascal-La Granja area are listed in Table 1. These 56 species are not of equal importance and abundance throughout the year, and their density varies from site to site. Some of these variables are expressed in Table 1. A select group of these species are also discussed further in Appendix 1.

TABLE 1. Insects that feed on *A. cornigera* in the Temascal-La Granja area. L=larva, A=adult, R=rare, O=occasional, V=very common, C=capable of feeding on occupied shoots, S=stopped from feeding by *P. ferruginea,* N=nocturnal feeder, D=diurnal feeder, Sh=most commonly eating shoot tips and very young leaves, M=most commonly eating mature leaves, and B=feeding on or in branches and/or trunk. They are divided by the season because their appearance on the acacia is closely correlated with the three seasons. It should be noted that the largest number of species are present during the time when the most active growth occurs in occupied shoots. Those species of particular significance to the ant-acacia interaction are discussed further in Appendix I.

COOL SEASON

(December - February)	
Lepidoptera	
Coxina hadenoides: Noctuidae	L, O, C, N, Sh
Occasional Arctiidae	L, O, S, N, Sh
Microlepidoptera in green thorns	L, O, S, ?, thorns
Orthoptera	
Montezumina oblongoculata: Tettigoniidae	A, O, S, N, Sh
Microcentrum rhombifolium: Tettigoniidae	A, O, S, N, Sh
Chloroscirtus sp.: Tettigoniidae	A, O, S, N, Sh
Coleoptera	
Chrysobothris sp. near *C. multistigmosa:* Buprestidae	A, O, S, D, MB
	L, V, C, ?, B
Onicideres poecila: Cerambycidae	A, R, S, D, B
	L, R, C, ?, B
Coscinoptera mucida: Chrysomelidae	A, O, S, D, ShM
Lechriopini, near *Lechriops* sp.: Curculionidae (Zygopinae)	A, O, C, D, Sh
	L, O, C, ?, thorns
Acanthoscelides oblongoguttatus: Bruchidae	L, V, C, ?, seeds
Mimosestes sp.: Bruchidae	L, V, C, ?, seeds
Stator subaeneus: Bruchidae	L, R, C, ?, seeds

WARM DRY SEASON

(March - May)

Lepidoptera	
Aristotelia corallina: Gelechiidae	L, V, S, N, Sh
Coxina hadenoides: Noctuidae	L, V, C, N, Sh
Microlepidoptera in the thorns	L, O, S, ?, thorns
Coleoptera	
Chrysobothris sp., near *C. multistigmosa:* Buprestidae	A, O, S, D, MB L, V, C, ?, B
Coscinoptera mucida: Chrysomelidae	A, R, S, D, ShM
Lechriopini, near *Lechriops* sp.: Curculionidae (Zygopinae)	A, O, C, D, Sh L, O, C, ?, thorns
The three Bruchidae listed above	
Heteroptera	
Mozena tomentosa: Coreidae	A, O, S, D, Sh

RAINY SEASON

(June - November)

Lepidoptera	
Coxina hadenoides: Noctuidae	L, V, C, N, Sh
Syssphinx mexicana: Syssphingidae	L, O, C, N, M
Aristotelia corallina: Gelechiidae	L, R, S, N, Sh
Norape sp.: Megalopigidae	L, V, S, N, ShM
Leaf rollers: Gelechiidae, Walshiidae, Geometridae	L, V, S, ?, ShM
Halisidota sp., probably *H. pura:* Arctiidae	L, O, S, N, ShM
Rosema dentifera: Notodontidae	L, O, C, N, M
Estigmene mexicana: Arctiidae	L, R, S, N, ShM
Iridopsis lurida: Geometridae	L, R, S, N, Sh
Euacidalia sp.: Geometridae	L, V, C, N, Sh
Semiothisa adjacens, S. puntolineata: Geometridae	L, O, S, N, Sh
Microlepidoptera in the thorns	L, O, S, ?, thorns
Thecla olbia, T. marsyas: Lycaenidae	L, R, C, D, ShM
Orthoptera	
Montezumina oblongoculata, Microcentrum rhombifolium, Chloroscirtus sp., others: Tettigoniidae (adults appear in late August)	L, V, S, N, ShM
Acrididae	L, O, S, D, ShM
Blattidae	A, R, S, N, Beltian bodies
Phasmatidae (adults appear in late August)	L, V, S, N, ShM
Coleoptera	
Pelidnota punctulata: Scarabaeidae (Rutelidae)	A, V, C, N, Sh
Diplotaxis denigrata: Scarabaeidae (Melolonthinae)	A, V, S, N, Sh
Anomoea sp., probably *A. rufifrons:* (Chrysomelidae)	A, V, S, D, Sh
Chrysobothris sp., near *C. multistigmosa* (Buprestidae)	A, V, S, D, MB L, V, C, ?, B

The three Bruchidae listed above	
Coscinoptera mucida: Chrysomelidae	A, V, S, D, Sh
Saxinus sp., probably *S. basilaris:* (Chrysomelidae)	A, V, S, D, Sh
Griburis decoratus, Pachybrachis sp., probably *P. femoratus, Cryptocephalus trixonatus, Urodera crucifera:* (Chrysomelidae)	A, V, S, D, Sh
Agrilus bicarinatus: Buprestidae	A, V, C, D, M
Pelidnota strigosa: Scarabaeidae (Rutelinae)	A, R, S, N, Sh
Phyllophaga vexata, P. anodentata, P. dasypoda, Diplotaxis microtishia: Scarabaeidae (Melolonthinae)	A, R, S, N, Sh
Euphoria leucographa: Scarabaeidae (Cetonniinae)	A, O, S, D, Sh
Cathartus annectens, Anchorius sp. near *A. lineatus, Hapalips* sp. near *H. lucidus:* Cryptophagidae	LA, V, C, ?, legumes
Lechriopini near *Lechriops* sp.: Curculionidae (Zygopinae)	A, O, C, D, Sh L, O, C, ?, thorns
Heteroptera	
Mozena tomentosa: Coreidae	LA, V, S, D, Sh
Homoptera	
Homalodisca coagulata: Jassidae	LA, V, S, DN, B
Oncometopia clarion: Jassidae	LA, V, S, DN, B
Dysmicoccus sp. in *D. neobrevipes* complex: Coccidae	LA, O, S, DN, B
Coccidae	LA, R, S, DN, M
Aphis medicaginis: Aphidae	LA, O, S, DN, Sh
Heteropsylla sp.: Psyllidae	LA, R, S, DN, Sh
Umbonia orozimbo: Membracidae	LA, R, S, DN, B
Diceroprocta sp.: Cicadidae	A, O, S, DN, B
Hymenoptera	
Acromyrmex octospinosus: Formicidae	A, O, S, DN, ShM
Solenopsis geminata: Formicidae	A, R, S, D, Beltian bodies

Seasonal abundance. The most obvious division is between those insect species that are present during the rainy season and those that are present during the cool and dry season (Table 1).

During the cool season (Dec. through Feb.) the density of active insects is much lower than during the rainy season. This is especially true of nocturnal insects. Of those that feed on *A. cornigera* during the cool season, there are only the larvae of *Coxina hadenoides*, adults of tettigoniid grasshoppers (*Montezumina oblongoculata, Microcentrum rhombifolium, Chloroscirtus sp.*, and others) *Onicideres poecila* (adults cutting shoots for oviposition), *Coscinoptera mucida,* and *Chrysobothris* sp., near *C. multistigmosa* (females ovipositing in damaged unoccupied shoots). However, the combined activity of *C. hadenoides* on occupied and unoccupied shoots, and the tettigoniid grasshoppers on unoccupied shoots, is sufficient to accomplish nearly 100 percent destruction of the shoot tips of *A. cornigera* that are emergent. Apparently due to the cool weather and subsequent dry weather, many of the damaged shoots, especially those over one year old, do not initiate new vertically lengthening branches until shortly before or after the first heavy rains in May.

From the return of warm weather in March until the first heavy rain on the 20th of May, the density (species and numbers) of active insects in the plant community decreases rapidly. By the first part of May, insect densities are less than one percent of those observed during the peak of the rainy season. Of those that feed on the shoot tips of *A. cornigera,* the larvae of *Coxina hadenoides,* the adults of *Mozena tomentosa,* the larva of *Aristotelia corallina,* and *Conscinoptera mucida* are sufficiently abundant to completely halt the height increment of only a small part of the unoccupied shoots in the 60-150 cm size class. Only *C. hadenoides* feeds externally on occupied shoots but its damage is considerable; it is doubtful that there was a single occupied shoot tip in the control subplots that grew continuously from 1 Mar. to 20 May without being fed on at least once by a larva of *C. hadenoides.* The larvae of *A. corallina* are very effective in removing the shoot tips of unoccupied *A. cornigera* in the 5-50 cm height range; on many sites where the surrounding vegetation is very low, and therefore the small acacias are fully exposed, 80-100 percent of the shoots have either the webbing or a larva of this moth on them during April and early May. The normal height increment rate of *A. cornigera* with intact shoot tips is undoubtedly slowed during the dry season. However, in those small local areas where neither *C. hadenoides* nor *A. corallina* are abundant, those shoots of *A. cornigera* with vertically lengthening shoot tips grow 15-60 cm in height during the dry season.

Most of the shoot tips produced by *A. cornigera* during the dry season are destined to become axillary tufts of leaves and flowering branches. These constitute the major part of the diet of *C. hadenoides, M. tomentosa,* and *C. mucida.* The removal of one of these shoot tips does not have the same effect on the plant as that of removal of a main shoot tip on a lengthening branch or central axis during the rainy season. It should be noted that the general vegetation surrounding the shoot is not increasing in height during the dry season and therefore the lack of height increment in the part of *A. cornigera* does not place the plant in immediate danger of being shaded by the surrounding plants. The surrounding vegetation is leafless and this allows sunlight to reach the lower leaves on the *A. cornigera* shoot. These leaves are shaded during the rainy season.

The remaining 47 insects listed in Table 1 are present during most of the rainy season. *Coxina hadenoides*, and *Mozena tomentosa* are much more abundant at this time. *Chrysobothris* sp., near *C. multistigmosa* adults are more common during the rainy season than the dry season but the larvae cause considerable mortality to unoccupied stumps throughout the year. Large populations of grasshoppers do not develop until the middle of August but these are also present through the cool season when most of the other rainy season insects have been gone for several months. The zygopine weevil and the microlepidoptera larvae in green thorns are present throughout the year but the weevil is present only as a larval stage in dry thorns during the dry season.

Host specificity. The insects listen in Table 1 can be divided into a group that may be found feeding on either unoccupied or occupied shoots, and a group that is virtually always found feeding on unoccupied shoots. The former group is composed of the larvae of *Syssphinx mexicana, Rosema dentifera, Coxina hadenoides, Euacidalia* sp., and green-thorn microlepidoptera, and the adults of *Pelidnota punctulata, Agrilus bicarinatus,* and the zygopine weevel. While it is not know with certainty that *Syssphinx mexicana, Rosema dentifera, P. punctulata,* and *Euacidalia* sp., are completely host specific on *A. cornigera,* they were not found on any other species of plant in the Temascal-La Granja area despite extensive searching. However, *Syssphinx mexicana, Rosema dentifera, Agrilus bicarinatus* and *Pelidnota punctulata* are recorded from areas (literature records and museum specimens as locality sources) where *A. cornigera* does not occur. *Coxina hadenoides* and the zygopine weevil are commonly found on *Acacia chiapensis. Coxina hadenoides* is occasionally found on *Acacia macracantha* but definitely prefers *A. cornigera* and *A. chiapensis* as a host plant in choice experiments.

The bruchids and cryptophagids in the legumes can not properly be placed in either group since they live for the most part outside of the sphere of activity of *Pseudomyrmex ferruginea.* The same can be said for nectar and pollen collecting Hymenoptera. They visit the plants frequently, when other sources are scarce, but are all species which are commonly seen visiting other species of flowers in the area.

The group normally found feeding on unoccupied shoots is much larger than the previously mentioned group. The 41 species in this group feed, with but two exceptions, on other species of Mimosaceae in the area as well as unoccupied *A. cornigera. Aristotelia corallina* has been found only on *A. cornigera.* As a population, *Mozena tomentosa* is believed to be host specific on *A. cornigera* despite the single female found feeding on *Mimosa albida.* Associated with this host specificity, *M. tomentosa* appears to be the most adept, of all the species in Table 1, at finding small unoccupied shoots of *A. cornigera* that are heavily obscured by the surrounding vegetation. When the ants are removed from a shoot, it is in great part the neighboring Mimosaceae that contribute phytophagous insects. With the exception of *Acromyrmex octospinosus,* the two *Thecla* species, *Pelidnota strigosa, Euphoria* *leucographa,* the scale, and *Dysmicoccus* sp. in the *neobrevipes* complex, the remaining 33 species are found feeding on *Acacia chiapensis* or *Acacia macracantha.* The Chrysomelidae, Lepidoptera, Orthoptera, *Diplotaxis denigrata,* and the two leafhoppers are commonly found feeding on *A. chiapensis* along with some other insects which are not found on *A. cornigera.* The Chrysomelidae, most of the Lepidoptera, Orthoptera, and *D. denigrata* are also found feeding on other species of Mimosaceae (*Calliandra houstoniana, Acacia farnesiana, Mimosa albida, Mimosa* sp.).

With the exception of the scales, mealy-bugs, and microlepidoptera, all of the insects feeding on unoccupied shoots are highly mobile in the stage found on *A. cornigera.* Associated with this, they are often known to move from plant to plant until they find one on which they are not molested by *P. ferruginae.* Under natural conditions, this search for a suitable host plant is sufficiently successful to insure that shoots of *A. cornigera* from which the ants have been removed begin to show phytophageous insect damage to the shoot tips and mature foliage in 1-2 days. In the treatment subplots in the experimental part of this study, the large groups of unoccupied shoots act as a trap for these insects. Their density per unit volume of plant community is considerably higher in some treatment subplots than in the neighboring plant community. However, the damage to unoccupied shoots scattered among occupied shoots (mixed subplots) is so severe that no differences are noted between the grouped and scattered unoccupied shoots.

Ant-tolerant insects contrasted with other insects. The nature and periodicity of the damage done are quite different between two groups of insects: those found normally on occupied and unoccupied shoots, and those found normally only on unoccupied shoots. Of those found normally on occupied shoots, *Rosema dentifera, Agrilus bicarinatus, Euacidalia* sp., the zygopine weevil, and the microlepidoptera larvae in the green thorns have no noticeable effect on the growth rate or condition of occupied *A. cornigera.* The effect of the bruchids on the seed crop is very great but it appears to be beyond the influence of *P. ferruginae. A. cornigera* normally exists in large numbers in spite of the high rate of seed destruction.

The other insects found on occupied shoots have a strong impact on individual shoots, but their cumulative impact on the entire population is low compared to that of the insects on unoccuped shoots. The larvae from a clutch of five eggs of *Syssphinx mexicana* usually strip an occupied shoot of its mature leaves. However, at any one site, only 0.5-3 percent of the shoots are defoliated by *S. mexicana* during the rainy season. Further, a single occupied shoot usually has enough mature leaves to rear the group of larvae to maturity after which they pupate without feeding on other shoots. A shoot defoliated by *S. mexicana* generally produces a new crop of leaves within two weeks and the probability of a single shoot being defoliated twice during the growing season is very small. Since the shoot tips are not eaten, the removal of the mature leaf crop does not noticeably affect the emergence of the shoot.

Pelidnota punctulata has more of an impact than *S. mexicana* on *A. cornigera* form and growth rate because it eats the shoot tips. The removal of all of the shoot tips by an adult *P. punctulata* (Fig. 26) is very detrimental to the height increment rate of the shoot. After the beetle moves to another plant, 1-2 weeks are often required for a new vertically lengthening shoot tip to reach the level of the older damaged shoot tip. The density of *P. punctulata* usually does not exceed six beetles per one hundred shoots and usually the density is 1-3 per one hundred shoots. In the experimental plots, at least 50 percent of the shoots did not have feeding damage of *P. punctulata* during the period 20 May through 8 Aug.

While *S. mexicana* and *P. punctulata* feed on the acacia only during rainy season, *Coxina hadenoides* is present in the larval stage throughout the year and has a heavy impact on the height increment rate at all times. It is a very rare occurrence that any one shoot of *A. cornigera* over 30 cm tall passes through an entire year of growth without having the main shoot tip eaten off by *C. hadenoides* at least once (Fig. 18). However, *C. hadenoides* is sensitive to the density of worker ants patrolling outside of the thorns; the frequency of feeding damage of this larva is inversely proportional to the density of workers outside of the thorns and the constancy of their patrolling (as affected by the size of the colony and the time of year and day). Therefore, the larger the ant colony, the longer there is uninterrupted vertical growth. It is largely due to *C. hadenoides* that weakly occupied shoots have height increment rates that are often less than one-tenth that demonstrated by heavily occupied shoots.

The damage inflicted by the three insect species listed above is normally received by occupied shoots and the population does very well in spite of it. At any given site during the rainy season where 90-100 percent of the readily visible shoots are occupied by mature colonies (the usual case), from 5-35 percent of the main shoot tips are destroyed by *P. punctulata* or *C. hadenoides* at any given time. However, the degree of damage stays relatively constant and the damage is rotated among the shoots. It can be said with certainty that during any part of the rainy season, the total number of vertically lengthening shoot tips present on a cohort of occupied shoots is 2-20 times the amount eaten during the same period by *P. punctulata* and *C. hadenoides*.

The damage inflicted by the individuals of insect species that feed on unoccupied shoots is less impressive than that described for the occupied shoots. However, the cumulative effect of the omnipresent diurnal and nocturnal defoliators of unoccupied shoots is much more severe than the effect of the relatively sporadic damage by the insects that feed on occupied

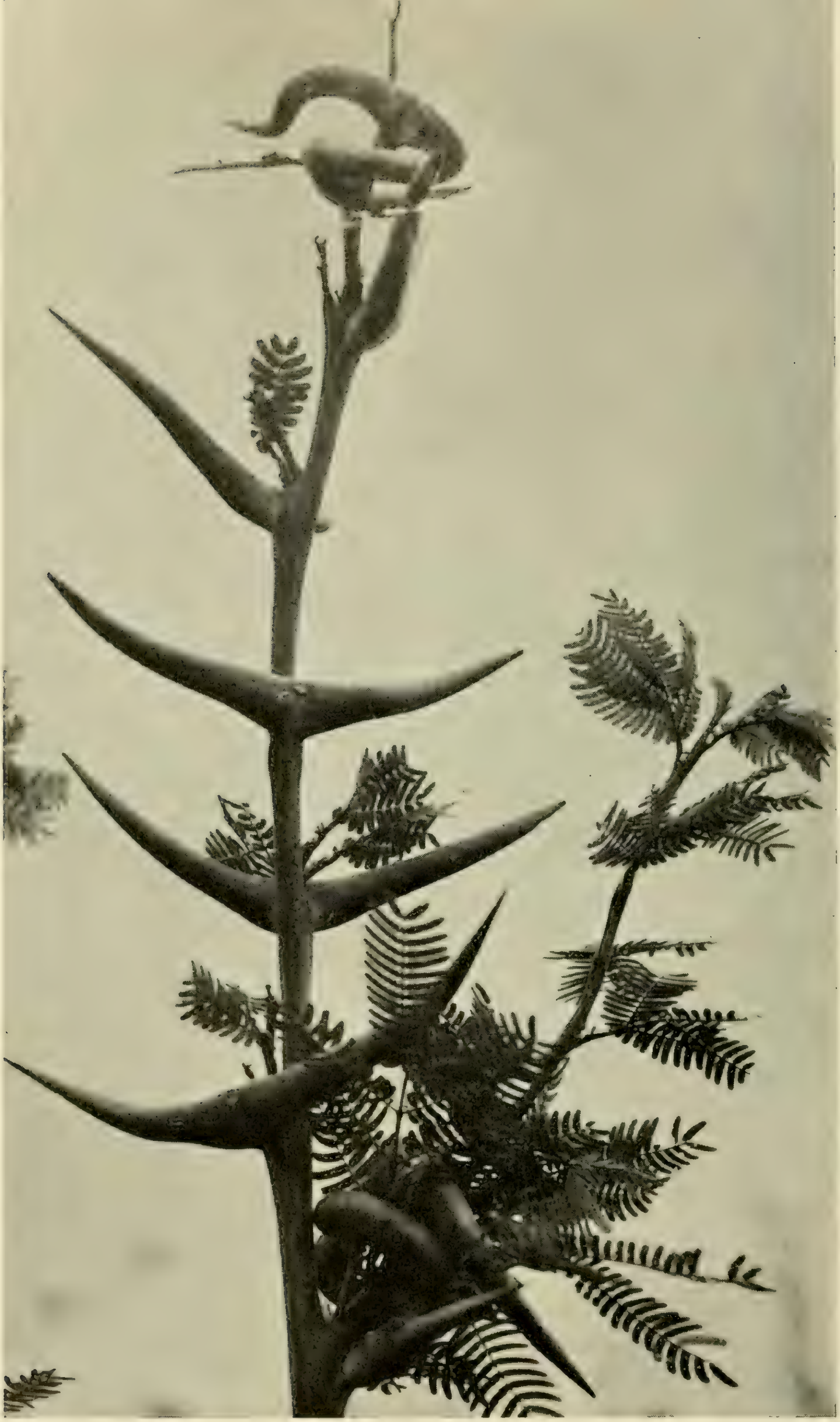


FIG. 26. The terminal end of the main axis of an occupied shoot of *Acacia cornigera.* The shoot tip of the main axis and the terminal axillary branch bearing the two type B thorns were eaten by an adult *Pelidnota punctulata.* The mature leaves were removed by a larva of *Syssphinx mexicana.* The short branch on the right that is growing out through the cluster of type B thorns is a flowering branch. Photo in subplot M-2 in June 1964.

shoots. Insect damage to unoccupied shoots is normally severe enough to kill the shoot either directly or indirectly after six months to two years. During the rainy season the diurnally active Chrysomelidae and *Mozena tomentosa,* together with the nocturnally active Orthoptera, Lepidoptera larvae, and Scarabaeidae generally remove 90 percent or more of the new axillary and terminal shoot tips as fast as they are produced. This is the case with both isolated and clustered (experimental plots) unoccupied shoots. Unoccupied shoots receive the usual damage from *S. mexicana, P. punctulata,* and *C. hadenoides,* but the density of these insects per unoccupied shoot is generally much lower than per occupied shoot. Unoccupied shoots rarely have the well developed succulent shoot tips that *P. punctulata* and *C. hadenoides* prefer as foods; they have already been eaten off. Unoccupied shoots often have so few mature leaves that the larvae of *S. mexicana* defoliate their shoot and wander off in search of more food.

In addition to the obvious damage to the foliage, it appears that the rate of new shoot tip production in unoccupied shoots drops off sharply 6-8 weeks after the rainy season begins. This was impossible to demonstrate conclusively because the removal rate by phytophagous insects is usually so high that it is not possible to determine how many new shoots have been produced over a given period of time.

One response to severe insect damage is flowering. Shoots in the 100-200 cm size range that are unoccupied from March through August produce many more flowering branches than do those that are heavily occupied. By July, most of the unoccupied shoots in this size range have some opening flowers on them and almost none of the heavily occupied shoots in this size range have flowers. Excessive flower production in shoots of this size and smaller, appears to be a reaction to the heavy and continuous damage to the unoccupied shoots. The majority of these unoccupied flowering shoots usually die before the end of the next dry season if they remain unoccupied, and therefore do not contribute to the reproduction of the population since it takes nearly a year for the seeds to mature.

Natural and man-made disturbance sites. Every species of insect in Appendix I was encountered at least once while feeding on unoccupied shoots of *A. cornigera* in both natural and man-made disturbance sites. In most arroyo and river-bank sites, the shoots are widely dispersed (up to 1000 m between shoots) in contrast to those in fields, pastures and roadsides. There is no evidence that wide spacing reduces the incidence of damage by defoliators of either the group of insects found on both occupied and unoccupied shoots or the group found only on unoccupied shoots. However, at lower insect densities this is probably not the case.

The shoots of *A. cornigera* in natural disturbance sites are usually among vegetation that is very irregular in height, species composition, and density.

Associated with this, many of the shoots are growing in partially shaded sites, rather than being either clearly emergent or submergent as is the usual case in the relatively uniform man-made disturbance sites. There appears to be a reduction in the frequency of Chrysomelidae, Buprestidae, Scarabaeidae, Lepidoptera, and Homoptera in these partially shaded sites as contrasted with sunny sites. A reduction in damage to foliage is, however, not noticeable. Variation in damage is difficult to evaluate because it is often so severe that maximal damage is present.

Certain defoliators of unoccupied shoots are correlated with different plant communities. The melolonthine scarabs which are such severe defoliators of unoccupied shoots at night during the first two months of the rainy season (especially *Diplotaxis denigrata*), are much more abundant in heavily grazed grass pastures. Orthoptera are much more abundant in the brushy pastures and ungrazed sites than they are in the open heavily grazed pastures. Chrysomelids are equally abundant in most sites but there are local variations in the species composition of those feeding on unoccupied *A. cornigera*. Lepidoptera and Homoptera are most easily observed feeding in the open heavily grazed sites but they are definitely present in the denser vegetation as well. *Mozena tomentosa* is undoubtedly the most omnipresent feeder on unoccupied shoots and its characteristic feeding damage (wilted shoots tips) is found in all types of sites at all times of the year. *Coxina hadenoides* is the most omnipresent feeder on both occupied and unoccupied shoots.

Heavily shaded unoccupied shoots are less severely attacked than are exposed ones. This is especially true of those growing under the dense vine tangle in ungrazed regeneration for the first 1-3 years after a fire or cutting. However, the rates of growth, and rates of recovery from damage, are so low that the undamaged shoot tips rarely become emergent. If and when they do, they are then rapidly eaten. The emergent shoot protruding above the general canopy is more readily found by phytophagous insects.

Other parts of the study area. With the exception of the Cotaxtla and Temascal-La Granja areas, populations of *A. cornigera* have not been examined intensively for defoliators in the study area. *S. mexicana, C. hadenoides, P. punctulata* and *M. tomentosa* were collected throughout the range of *A. cornigera* in the study area with sufficient frequency to indicate that they were probably present throughout. Judging from the damage found on unoccupied shoots in other areas the feeding pressure of phytophagous insects is as great as in the Temascal area, even if the same species are not involved.

In the Cotaxtla area, with a few exceptions, the species listed in Appendix I have been recorded from either direct observation or the finding of damage. The Cotaxtla area has more acreage of pasture and the pastures are more heavily grazed than in the Temascal-La Granja area, and therefore the population structure of *A. cornigera* differs somewhat. However, the incidence of insect damage to unoccupied shoots is, if anything, higher than in the Temascal area. This appears to be associated with the very exposed nature of many of the shoots in the open pastures.

Insects reported in the literature. Wheeler (1942) lists the insects reported in the literature as feeding on various swollen-thorn acacias, or being associated with them in some manner. No insects are recorded specifically for *Acacia cornigera* but two are recorded from Misanhtla, Veracruz from *Acacia* sp. It is likely that the acacia referred to is *A. cornigera. Bruchus* sp. is recorded from the legumes and *Adelocephala xanthocroia* is recorded as entering the exit hole of the *Bruchus* sp. to feed on the pulp in the legume. The bruchid is probably *Acanthoscelides oblongoguttatus* or *Mimosestes* sp. It is likely that the feeding habits of *Adelocephala xanthocroia* are incorrectly recorded since the exit hole of the bruchid is three or less millimeters in diameter and *A. xanthocroia* larvae quickly reach a diameter of 5-10 mm.

It is interesting that in Wheeler's list of 54 species of arthropods there are only 13 which could possibly act as defoliators. Of these 13, only five are likely to feed on swollen-thorn acacia foliage or fruit. This list refers to all the species of swollen-thorn acacias known to Wheeler and it is very small for a group of common plants that range from north-western and north-eastern Mexico to Panama and Colombia. Studies in progress show that such a list should contain several hundred species of insects.

Sampling problems. The insects on the shoots in this study were found by visual searching; shoots were not beaten over a sheet or surveyed in other ways because the shoots were for the most part in experimental plots and could not be disturbed. The undersides of the leaves were examined but not as thoroughly as the upper sides. When searching at night with a flashlight, it is especially difficult to locate insects on the trunk and interior part of the canopy. It is necessary to examine a shoot from above and/or on all sides. Shoots over 250 cm tall are not easily examined, and the list of insects in Table 1 undoubtedly omits some of the species that feed on taller shoots, since no observations were made on insects feeding on shoots over 5 m tall. However, feeding damage characteristic of the species on shorter trees is definitely present on these taller shoots.

It is probable that more than 80 percent of the species of insects that regularily fed on occupied and unoccupied *A. cornigera* in the Temascal-La Granja area are included in Table 1. There are many other species of insects, representing at least 23 families, that are seen on the foligae of unoccupied shoots; these are not listed as there is no evidence that they feed on *A. cornigera*.

Mammals as defoliators. In addition to the insects listed in Table 1, there are some mammals in the Temascal area that eat the foliage of *A. cornigera* under certain circumstances. In no case examined was the interaction between ant, acacia and mammal found to be as clear as that between ant, acacia and insects. The brocket deer (*Temazate: Mazama americana temama*), burro, horse, and cow were examined in this context. Of prime importance was the determination if these animals would eat *A. cornigera* in the absence of *P. ferruginea.* None of these animals have the direct impact on *A. cornigera* that phytophagous insects do, but cattle may drastically alter the structure of the vegetation and thereby have a strong indirect effect on *A. cornigera.*

Brocket deer. In past years, brocket deer have been common in the Temascal area, and their tracks were occasionally seen during this study. There is no evidence that they entered the experimental plots. Since they could have been an important herbivore in past years, the following observations were made to determine the reaction of a brocket deer to *A. cornigera* and *P. ferruginea.* A tame female (three years old) was used; she had never been allowed to feed outside of the owner's yard and he was convinced that she had no previous experience with *A. cornigera.*

She readily ate shoot tips and mature foliage from *A. cornigera* that did not have ants outside of the thorns (Fig. 17). These lateral branches (40-70 cm long) were cut from occupied shoots, and the ants shaken and picked off. The branches had fully developed type A thorns, intact mature leaves, and undamaged shoot tips. The deer nipped off the shoot tips and mature leaves with its molars or incisors. Large mature leaves often have raches or petioles that are too tough to bite through with the incisors, so the deer shifted her head and bit them off with her molars. The leaves project 7-15 cm past the tips of the thorns and her thin face fit easily between the widely spaced halves of the swollen thorns. She rarely shifted her feeding position as a consequence of being stuck by a thorn. Occasionally, a dry and hard swollen thorn was bitten off with the molars and chewed up with the leaf. On one occasion, she ate 40 inflorescences that had been hand-picked from *A. cornigera.*

When feeding on unoccupied *A. cornigera* and on other plants, she fed rapidly. On one occasion, she ate 50 mature leaves and five shoot tips from five branches in 12 minutes. As soon as she finished one branch, another was offered. She would eat 15-50 shoot tips (5-10 cm long) as fast as they were offered. The deer would not feed indefinitely on *A. cornigera* alone, but when shoots of this were alternated with other acceptable plants, she would eat until satiated.

Of the foods offered her, she had definite preferences. *A. cornigera,* Malvaceae, Convolvulaceae, Leguminosae (*Mucuna pruriens* and other vines), grass inflorescences, and sedge inflorescences were readily accepted.

When first feeding after a night without food, she would eat foliage of *Acacia macracantha, Acacia chiapensis* and *Acacia farnesiana*; later she refused these after having eaten a small amount of other foliage. Even after two days of starving, she would not eat foliage (shoot tips or mature leaves of *Solanum torvum, Bixa orellana, Croton glabellus, Eupatorium odoratum, Calliandra houstoniana,* and *Bauhinia ungulata.* These six plants are all shrubs that are commonly found in heavily grazed cattle pastures.

It can be said with some assurance that the foliage of *A. cornigera* is not distasteful to the brocket deer, and that the type A thorns on lateral branches do not deter it from feeding. Following a number of days of feeding the deer unoccupied foliage, she was offered a branch about 1 m long that was swarming with excited workers of *P. ferruginea.* This was in the early morning after the deer had passed the night without food. She was normally not allowed to feed at night. She began to nip the leaves from the branch immediately. Several ants ran onto her nose and facial region and began to sting her. She stopped feeding, turned her head away, and by the use of her very long and flexible tongue, and sharply pointed forefoot, removed the ants. She then returned to the branch and began to feed again. Again the ants ran on her and again she stopped feeding to remove them. This was repeated 2-3 times before she finally turned and walked away from the branch, leaving about one-half of the leaves still intact. About 15 minutes later a new branch was offered to her with ants on it, and the same pattern was repeated.

This experiment was repeated four times that morning at 15 minute intervals, and each time her reaction was the same. On two following occasions, 3 and 4 days later, the same experiment was tried again. In each case the same thing occurred. The deer always reacted to the ants by turning casually or suddenly away from the branch and removing the stinging ants with her tongue or forefoot. She removed all ants before she resumed feeding; she was very sensitive to the presence of an ant biting her, stinging her, or just running on her hair.

There were two immediate effects of her reaction to *P. ferruginea.* Some leaves were often left on the branch, and she required 3-10 times as long to remove the leaves that she did eat. However, the greatest apparent significance of this form of feeding deterrence is in neither of these direct effects. In natural circumstances, where there are a large number of species of plants to choose from, any factor that causes the deer to turn away from the plant is of significance to the plant; it is unlikely that she would return to the same plant immediately. A second point of consideration in the case of *A. cornigera* is that since the deer can only reach vegetation which is less than about 1.5 m tall, any shoot taller than this would have the most important part of the foliage (shoot tips) above the deer's foraging range.

Burro. A six year old female burro refused to eat loose leaves, or leaves off of branches, of unoccupied *A. cornigera.* These were offered many times between September 1963 and July 1964. She rejected the foliage either on seeing or smelling that it was *A. cornigera.* She did not contact the thorns before turning away. Since she sniffed at the offered foliage, it is likely that she recognized it by smell. When leaves of *A. cornigera* were cut and offered mixed with the leaves of grasses, mints (Labiatae) or guacimo *(Guazuma ulmifolia),* the acacia leaves were usually spit or sorted out of the mixture, and the other leaves eaten. Occasionally, the acacia leaves were chewed and swallowed with the other plant matter. This burro had previous experience with occupied *A. cornigera* since there were several thousand shoots of *A. cornigera* in its pasture. Since she did not eat the foliage consistently under any circumstances, it is impossible to determine if her refusal of *A. cornigera* is purely a function of chemical properties of the acacia or is in some way connected with the presence of *P. ferruginea.*

Behind the laboratory at Temascal, another female burro grazed around 20 potted unoccupied seedlings of *A. cornigera* for about one month. She never fed on the plants. However, her weanling burro was sampling plants behind the laboratory and ate four of the seedlings in entirety. Each shoot had 2-5 fully developed swollen thorns on it that contained founding queens. The leaves, stems and thorns were chewed thoroughly and he made no attempt to spit them out. Shortly after he was observed to try, and then reject, foliage of *Callinadra houstoniana* and *Bauhinia ungulata.* This indicates that the foliage of *A. cornigera* is in itself not distasteful to young burros, despite the fact that adult burros long exposed to ant-inhabited acacias were very unwilling to eat it. In view of the reaction of the brocket deer to *P. ferruginea,* it can be surmised that the avoidance of the foliage of *A. cornigera* by burros is learned and enables them to avoid contact with *P. ferruginea.*

A simple test of this was conducted. The air blown through a thoroughly washed aspirator into the nose of a six year old female burro caused no reaction. However, when the aspirator was filled with 100 workers of *P. ferruginea,* the burro rapidly jerked her head away from the stream of air. Ants were not being blown onto the burro. This experiment was repeated several times a day for three days; after this time, she also jerked her head away from the stream of air from a clean aspirator. It is of course possible that the alarm odor of the ants (discussed in a later section) was merely an unpleasant odor to the burro. It is also possible that the alarm odor served as an indicator of the presence of *P. ferruginea*; when a large mammal comes near to, or brushes against, a heavily occupied shoot of *A. cornigera,* the alarm odor can be distinctly smelled at a distance of a meter or more and might serve to identify the acacia at night.

Cattle. During the cool season, cattle will, on occasion, browse on *A. cornigera*. In January, members of Farfan's and Torrealva's herds of cattle were observed seeking and eating foliage from standing shoots of *A. cornigera* in the 1.5-4 m height range. Since the weather was cool (13-23° C.), there were almost no workers of *P. ferruginea* outside of the thorns. The cattle were eating mature leaves from lateral branches 1-2 m above the ground (Fig. 27).

The availability of alternative foods at this time of year is very difficult to evaluate. Some grasses, Convolvulaceae, Leguminosae (vines) and other readily accepted plants are still green and are eaten by cattle. Certainly the volume of food available is less at this time than during the rainy season, but it is also more than during the latter part of the dry season; during this warm dry period the cattle do not normally browse on *A. cornigera*. During the following weeks, until the warm season began, these cattle were frequently observed feeding on standing *A. cornigera*. A single cow would remove

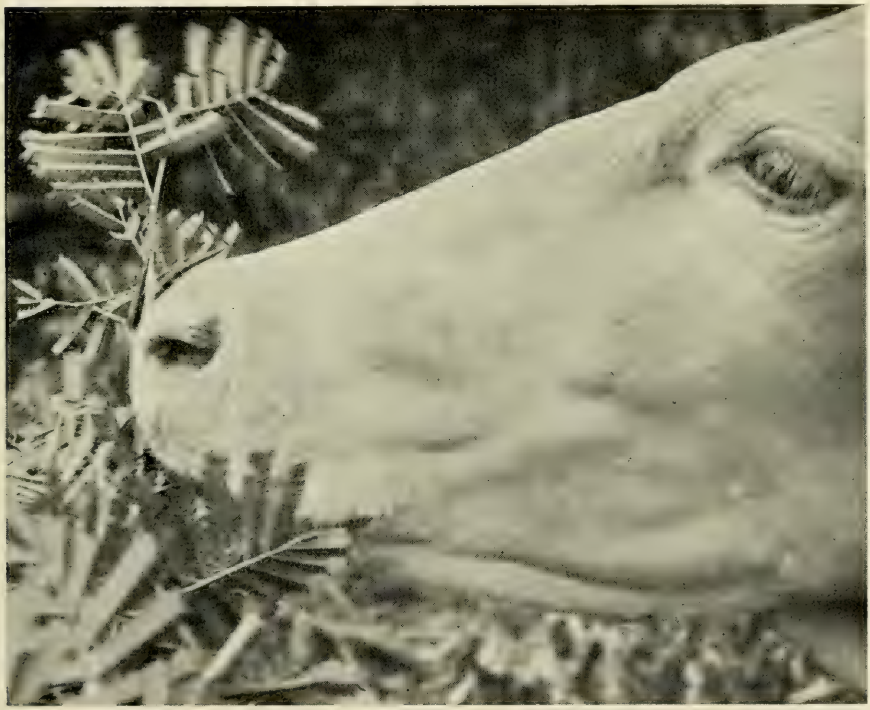


FIG. 27. A seven year old cow browsing mature foliage on lateral branches of a tall unoccupied shoot of *Acacia cornigera* during the cool season (January 1964) in one of Juan Torrealva's pastures. A colony of *Pseudomyrmex ferruginea* was living in the thorns of this shoot but it was too cold for the workers to be active outside of the thorns. This same cow was observed to browse mature foliage from heavily occupied tall shoots that had been cut with a machete in July 1964.

0.25-25 percent of the mature leaves from a shoot that were less than 2 m above the ground. During the rainy season, these cattle do not normally browse standing shoots of *A. cornigera.* However, they were occasionally observed to eat a shoot tip or mouthful of mature foliage from both occupied and unoccupied shoots.

During the cool season, these cattle also followed people cutting brush. At this time there was a large amount of green foliage above the browse line, and by following the workers, the cattle could get this food. The foliage from occupied canopies of *A. cornigera* was sorted out by the cattle and eaten from the piled mixture of *Croton glabellus, Bauhinia ungulata, Mimosa albida, Helicteres guazumifolia, Coccoloba* sp., and other 2-4 m tall shrubs. It should be noted that at this time of year, occupied shoots of *A. cornigera* have reduced ant populations on the surface of the shoot.

During the rainy season, the five oldest cattle in Torrealva's herd came to the canopy of any cut tree and began to browse. This was especially noticeable in the case of large trees. The cattle were apparently attracted by the sound of cutting and the movement of the other cattle toward the fallen tree. The leaves of some of these trees are not normally eaten when the tree is standing even if the leaves are within reach. In this case *(Ateleia pterocarpa, Tabebuia pentaphylla, Bauhinia ungulata),* the cattle stop feeding after a couple of mouthfulls. On the other hand, *Guazuma ulmifolia* and *Cordia alliodora* are eaten readily, whether the tree is standing or cut. *A. cornigera* is a special case; at this time of year (Jul.) it is almost never browsed when standing, but when cut it is readily browsed. The cut *A. cornigera* shoots had mature foliage growing at ground level and the cattle had grazed on many other species of plants within a few inches of this foliage. When the acacia was cut, it was not stripped of all its foliage by the cattle, but 10-75 percent of the mature leaves and shoot tips were often eaten. These shoots normally had a thousand or more ants on their surface at the time the cattle were feeding, but relatively few of these ants found their way onto the cattle due to the disorganization of the colony on a newly cut acacia. The cattle did not show an obvious response to the few ants that found them. It appeared that the ant was not able to sting through the skin either on the bare nose or the hairy face to a sufficient depth for the cow to feel it. The cow's nose was surprisingly tough or insensitive; needle-sharp spines sticking into it often did not cause her to turn away.

The thorns of *A. cornigera* do not noticeably affect the cattle. They do not recoil when stuck in the nose or cheek. A cow's long tongue reaches around and behind the leaf, and plucks it from the branch by pulling it toward her. Occasionally the leaf petiole is cut with the incisors. Entire new green branches up to 40 cm long are sometimes eaten. When a cow has her head well among the foliage and finds herself being stuck when withdrawing, she closes her eyes until her head is free.

When the cattle were feeding on standing *A. cornigera* during the cool season, it was impossible to determine their reaction to *P. ferruginea* since the shoots had very reduced ant populations outside of the thorns. During the warm part of the year, both before and after the cool season, the cattle were only very rarely observed to browse standing shoots of *A. cornigera*. In the case of both occupied and unoccupied shoots, they usually turned away from the shoot after a mouthful. However, on one occasion in late April, an adult cow was observed to browse the mature leaves from unoccupied shoots in treatment subplot N-1 for nearly 15 minutes. The cow moved from shoot to shoot and did not eat more than five leaves from any one shoot. On several occasions in the general area of plots N and O, cattle in Farfan's herd were observed to start to take a mouthful of foliage from heavily occupied low shoots, but then turn their heads away without taking any further leaves. There were large numbers of excited workers on the surface of these shoots.

When the branches or leaves of *A. cornigera* were offered to any of these cattle, they were usually rejected even when offered as alternative members of series of highly acceptabl plants (*Guazuma ulmifolia, Cordia alliodora,* grasses, Labiatae, Convolvulaceae, and Fabaceae (vines)). When small branches of *A. cornigera* foliage (both de-spined and with thorns) were offered as a mixture with grass or other acceptable plants, the *A. cornigera* was usually sorted by taste and/or by vision from the bunch. The acacia was not accepted, or if accepted it was often spit out. However, two old cows were found that would eat equal mixtures (by count) of leaves picked from *A. cornigera* and *G. ulmifolia*.

In summary, it can be said that at least under certain circumstances, a brocket deer, a young burro, and numerous cattle ate the foliage of *A. cornigera*. At least to these animals, it is not as distasteful as other plants that are commonly left unbrowsed in these animals environment. This suggests strongly that the repeated avoidance of *A. cornigera* by browsing mammals may be due to some other factor than the taste of the plant itself. Part of this avoidance factor maybe due to the aggressive behavior of *P. ferruginea*, but considerable experimentation is necessary to settle the matter.

CONTRAST OF A. CORNIGERA, A. SPHAEROCEPHALA, AND A. CHIAPENSIS. While *Acacia cornigera* is separable from *Acacia sphaerocephala* on the basis of inconspicuous but relatively consistent details of external morphology, *Pseudomyrmex ferruginea* treats them as if they were the same species of plant. The thin-walled legume characteristically found on *A. sphaerocephala* is indistinguishable from the thin-walled type of legume found on *A. cornigera* in the Temascal area. The short inflorescence of *A. sphaerocephala*

(Fig. 5a) is very similar to that of *A. cornigera* (Fig. 1a). It has the same floret length and density, position on the shoot, and peduncle with a large diameter. Though usually lacking nectaries on the leaf rachis, occasional plants of *A. sphaerocephala* have been found with 1-3 nectaries distal to the petiolar nectary. The petiolar nectaries of both species are indistinguishable in gross morphology. The Beltian bodies of *A. spaerocephala* differ from those of *A. cornigera* only in that those of the former are slightly broader and have less red epidermal pigment. With the exception of the bicolored thorns and completely untwisted type B thorns found in many parts of the range of *A. sphaerocephala,* subpopulations and individuals of *A. cornigera* have been found that display almost every variation in thorn form that is known in *A. sphaerocephala.* While *A. cornigera* does not develop into low dense mats of vegetation like those of *A. sphaerocephala* on sand dunes (Fig. 5b) even when growing on sand dunes, there are many areas where *A. sphaerocephala* has an upright life form.

The principle ecological difference between these two species is that within the study area, *A. cornigera* is a plant of wetter areas and *A. sphaerocephala* is a plant of drier areas. Within each of their respective ranges, *A. cornigera* and *A. sphaerocephala* have expanded into man-made disturbance sites in the same manner and here they play ecologically equivalent roles in the plant community. That they are two distinct species, and not merely two forms associated with two different rainfall regimes, is shown by the following facts. In areas where the species are sympatric, they flower at different times of the year, and the plants are morphologically distinct from each other. Apparent hybrids are rarely encountered. There is no doubt that the plants determined to be *A. cornigera* and *A. sphaerocephala* in the study area are properly associated with their type specimens.

A. cornigera has a much greater range than *A. sphaerocephala* but both species are about equivalent in respect to the amount of morphological variation per unit area of range. While these two species seem very closely related, sufficient evidence is not yet available to postulate the actual course of events that has led to their distinctness.

A. cornigera and *A. sphaerocephala* are much more similar to each other than either is to *Acacia chiapensis. P. ferruginea* does not interact with *A. chiapensis* in the same manner as it does with *A. cornigera* and *A. sphaerocephala.* At any particular site, *A. chiapensis* is extremely variable in respect to morphology and life form. The individual plants can be arranged from those that are phenotypically similar to the sword-thorn acacia, *Acacia macracantha,* to those that look like hybrids between *A. chiapensis* and *A. cornigera* (Fig. 3a).

The similarity of the hybrids to *A. macracantha* is based on the 1) pale green leaves; 2) straight, thin, and slightly flattened thorns which are dark brown, swollen, and have a tough, central parenchyma; 3) very low ratios of swollen thorns to small stipular thorns; 4) spreading life form with the shoot canopy as wide as the shoot is tall; 5) extremely bitter tasting foliage that has little insect damage to the shoot tips; 6) very low number and small size of Beltian bodies produced per leaf (*A. macracantha* lacks Beltian bodies); and 7) fact that the shoot is invariably not occupied by a self-sufficient unit of *P. ferruginea* but always has founding queens of *P. ferruginea* and many thorns previously opened by founding queens (*A. macracantha* thorns are only very rarely entered by *P. ferruginea* queens).

The similarity of the hybrid plants, at the other end of the range of variation, to *A. cornigera* is based on the 1) dark green leaves; 2) thick and round dark brown thorns that occasionally are curved and have soft central parenchyma; 3) very high ratio of swollen thorns to small stipular thorns; 4) slender life form with most thick branches being vertical; 5) bland tasting foliage that often exhibits repeated damage to shoot tips by insects of the same species that feed on unoccupied *A. cornigera;* 6) medium number and normal size of Beltian bodies per leaf; and 7) fact that the shoot is almost invariably occupied by a unit of *P. ferruginea* whose size is proportional to the number of Beltian bodies produced by the shoot.

While it is plausible and likely, sufficient evidence is not available to support the hypothesis that the plants which are phenotypically similar to *A. cornigera* are in fact exhibiting the expression of genes or chromosomes gained through occasional crossing between the two species. The same genera of bees pollinate both species. In the Temascal area, most shoots of *A. chiapensis* flower in January through March. However, occasional shoots of both species are found in flower in all months of the year.

Before the existence of man-made disturbance sites in the Temascal area, *A. cornigera* and *A. chiapensis* grew as scattered and mixed populations on river banks and in arroyos, based on observation of the few remaining undisturbed sites. When man entered the area, *A. cornigera* spread rapidly into the fields, pastures and roadsides. *A. chiapensis* has stayed in the natural disturbance sites and is now relatively much rarer than *A. cornigera.* A major reason for this is that while dissemination of seeds of *A. cornigera* by birds is very common, there is no evidence of overland seed dispersion of the seeds of *A. chiapensis* by birds. In the latter species the seeds are imbedded in a dry and to me, tasteless pulp. The legumes of *A. chiapensis* often drop from the shoot before they completely dehisce and they will float for at least an hour; they are most likely normally water dispersed.

There is a second reason why *A. cornigera* has spread much more rapidly than has *A. chiapensis.* Like *A. cornigera, A. chiapensis* needs full sunlight for normal growth. Man-made disturbance sites often grow a dense shading canopy very rapidly. When occupied by a colony of *P. ferruginea, A. corni-*

gera is quite capable of growing fast enough to keep above the rapidly growing surrounding vegetation. As one moves across the range of variation of *A. chiapensis*, from being phenotypically like *A. macracantha* to being phenotypically like *A. cornigera,* the ability to produce a large annual vertical height increment increases; the susceptibility to insect destruction of the shoot tips also increases. However, these rapidly growing plants are not able to sustain an ant colony large enough to insure freedom from insect damage. Therefore, most of the *A. chiapensis* shoots do not grow fast enough to remain above the surrounding canopy. In natural disturbance sites, the canopy is generally more interrupted and the plants are often able to lean out toward the water. In these areas the slowing of growth by insect damage is not so serious to the plant due to the lack of shading plants.

Within the study area, *A. cornigera* has a much greater geographic and ecologic range than does *A. chiapensis*. *A. chiapensis* appears to be much more closely related to the Guatemalan *Acacia donnelliana* Saf. and the Costa Rican and Panamanian *Acacia melanoceras* Beurling than it is to either *A. cornigera* or *A. sphaerocephala*.

In respect to the members of the genus *Acacia* as a whole, the swollen-thorn acacias possess a distinct set of characteristics. If those swollen-thorn acacias which are consistently found to be occupied by some species of *Pseudomyrmex* are separated as a group from those which are inconsistently found to be occupied by some species of *Pseudomyrmex*, then *Acacia cornigera* can be regarded as representative of the former group and *Acacia chiapensis* as representative of the latter group. This is not to say that *A. cornigera* is equal in all quantitative respects to a plant such as *A. sphaerocephala* but rather that it is very similar to it in qualitative characteristics.

Foliar nectaries are commonplace throughout the genus *Acacia* in Mexico and Central America. However, they do not reach the degree of morphological proliferation in other species that is attained by those of the swollen-thorn acacias. *A. cornigera* and *A. sphaerocephala* undoubtedly produce more nectar per leaf than do any other acacias in the study area.

The leaves and their products are essential to growth and survival of the ant colony. While *A. cornigera* leaves do not generally remain on the shoot for more than a year, it is notable that during the dry season the loss of leaves is gradual. New leaves are continually produced in axillary tufts so that living shoots are rarely leafless. The leafless condition is common during the peak of the dry season in other acacias in the study area and especially those that are sympatric with *A. sphaerocephala*.

Within the study area, Beltian bodies are peculiar to the swollen-thorn acacias. A shoot of *A. cornigera* that is growing in full sunlight, occupied by *P. ferruginea* and over two years old, produces a Beltian body on the tip of every leaf segment. Within its life span, *A. cornigera* undoubtedly produces more weight of Beltian bodies than either *A. sphaerocephala* or *A. chiapensis.* In contrast to the usual case with leaf parts, Beltian bodies have a very high nutritive value; yet there is no evidence that their production by the plant is of direct value to the plant itself. They possess a vascular trace and appear to be a modification of the tip of the leaf segment rather than an outgrowth of the leaf margin. The rate of leaf production during the dry season is less than 20 percent of that during the rainy season. But since small numbers of new leaves are produced as leaf tufts in thorn axils, small numbers of Beltian bodies are produced on many shoots during the dry season.

Within the study area, there are five species of acacia that regularly bear stipular spines which are over 3 cm long. Of these, *A. cornigera, A. sphaerocephala,* and *A. chiapensis* are regarded as swollen-thorn acacias; *Acacia macracantha* and *Acacia farnesiana* are not placed in this group because they do not have swollen thorns, are not inhabited by ants, and do not produce Beltian bodies.

Of these five species, *A. cornigera* produces the largest volume of space in its thorns (although *A. sphaerocephala* may rarely do just as well). As much as one-half of this volume may be contained in the type B thorns which are highly twisted back on themselves and are not located in the area of most new leaf production. Both type A and type B thorns are much shorter than their leaves. Both cattle and the Brocket Deer are not deterred from eating mature leaves by the presence of the type A thorns on lateral branches (Fig. 17 and 27). The long tongue of the cow and the long narrow face of the deer are both well suited to reaching between the short, widely spread thorns to remove leaves. The thorns contain considerably more lignified tissue than is necessary to make them as strong as those of the same length that are produced by *A. macracantha.* However, this lignification is necessary if the thorns are to contain a large internal lacuna and still be as strong as the solid thorns of *A. macracantha* which are much thinner. While new swollen thorns are generally not produced by *A. cornigera* or *A. sphaerocephala* during the dry season, they are produced with great regularity during the rainy season. *A. chiapensis* is less consistent in its rate of production of swollen thorns.

A. cornigera appears to have the highest growth rate of any species of acacia in the study area. This applies to both lengthening of specific branches and to shoot height increment. Such a trait is important to a plant which is dependent on full sunlight for normal maturation and yet must attain this maturation while growing among vegetation which is constantly rising in height and producing heavy shade. Possession of a very tender shoot tip that lacks fibrous tissue, and external epidermal modifications for protection, is apparently associated with the very rapid rate of branch elongation.

To the author's taste, the shoot tips of *A. cornigera* and *A. sphaerocephala* have a pleasant bland flavor. The shoot tips of the pale-leafed form of *A. chiapensis* are very bitter to the author's taste. The shoot tips of *A. macracantha, A. farnesiana* and seven unidentified species of *Acacia* in the study area are likewise very bitter tasting. Apparently associated with the physical tenderness and relative lack of distinctive flavoring compounds of the shoot tips *of A. cornigera,* they are accepted as food by a number of insects that normally feed on other species of plants. It is also eaten by a cricetid rodent, the Brocket Deer, and livestock. Loss of foliage to these phytophagous animals takes place only under special circumstances, if a large colony of *P. ferruginea* lives in the shoot. It is almost guaranteed to take place if the shoot is unoccupied.

A seedling of *A. cornigera* or *A. sphaerocephala* requires at least three full growing seasons before it will flower in the following dry season. The first early flower crop is produced in the fourth dry season. A sucker of *A. cornigera* from a large stump may flower when only nine months old but it usually does not flower until the end of its second dry season. The seed does not mature until 10 to 12 months after flowering. *A. chiapensis* seedlings and regenerating suckers require one to two years longer to flower for the first time and the seeds mature at the time of the next year's flowering. In natural disturbance sites, reproduction of *A. cornigera, A. sphaerocephala,* and *A. chiapensis* occurs often from direct growth from seeds as it does from suckers from cut or burned stumps. Yet in man-made disturbance sites that are repeatedly cleared, these three swollen-thorn acacias are heavily dependent upon regeneration from root stock to maintain their existing densities.

Throughout the study there has been no evidence that indicates that any of the traits described above are directly dependent upon the presence of a colony of *P. ferruginea* for their expression.

APPENDIX I. DETAILS OF DEFOLIATOR ACTIVITIES

Mozena tomentosa Ruckes.

Mozena tomentosa is a 2cm long brown coreid bug. The adults are present all year and both adults and nymphs are very common during the rainy season. They feed both day and night and suck the sap of the terminal and penultimate leaf rachis and shoot tips of *Acacia cornigera.* This causes permanent wilting of the portion of the leaf distal to the puncture and cessation of growth of the punctured shoot tip. A cluster of 3-15 nymphs or 1-4 adults may feed on one shoot tip or axillary tuft of new leaves. With the exception of one female on the shoot tip of *Mimosa albida, M. tomentosa* was not found feeding on other species of plants. The adults are very adept at locating young *A. cornigera* shoots that are submerged in dense second growth, and are responsible for the wilted shoot tips that are very commonly found on young shoots that are not occupied by a worker force of *P. ferruginea.* In an experimental plot where the acacia sucker shoots were nearly dead following nine months of defoliation by all types of phytophagous insects (H-1), *M. tomentosa* were often the only insects that were still attracted to the tough and calloused branches that were still living. It found the new axillary buds almost as soon as they appeared above the epidermis. During the dry season, *M. tomentosa* adults, larvae of the noctuid *Coxina hadenoides,* and larvae of the gelichiid *Aristotelia corallina* were the three major active defoliators of *A. cornigera.*

Workers of *P. ferruginea* readily attacked adults and nymphs of *M. tomentosa*. If the workers invaded a shoot on which a bug was feeding, it sometimes required repeated attacks by single workers to induce the bug to withdraw its mouthparts and leave. Occasionally ants wiped their mouthparts on the leaf surface following these attacks. When a bug lit on a shoot tip that was being patrolled, it was immediately attacked and departed. On 12 July 1964, an adult female of *M. tomentosa* was placed on the shoot by the author. She was bitten 18 times in 62 seconds as she fell from branch to branch and finally flew off the occupied shoot.

Umbonia orozimbo Fairm.

Umbonia orozimbo is a 6 mm long green and red membracid. The adults were present on *A. cornigera* all year and the nymphs were found from Aug.-Jan. (Fig. 28). Adults were also found feeding on the stems of *Acacia chiapensis* and *Acacia macracantha*. While not abundant in the adult stage, on two occasions a female was found with her brood of nymphs feeding on the main vertical branch 20 cm below a wilted shoot tip. *U. orozimbo* was found both in experimental plots and on shoots that had naturally lost their colony. When a stem covered with nymphs was bent over to contact a queen-shoot occupied by *P. ferruginea*, 82 nymphs and the female were forced to jump off in 2 minutes and 42 seconds due to biting and stinging attacks by the worker ants.

Pelidnota punctulata Bates

Pelidnota punctulata is a 25 mm long rutelline scarab with yellow elytra and a green to brown pronotum. The adults were common from June through September; they fed on the shoot tips of *A. cornigera* only at night. Neither the bettle or its feeding damage was found on other species of acacia. During the day, the beetles rested in the most heavily shaded part of the shoot and this was usually toward the center of a mass of type B thorns. *P. punctulata* ate the shoot tips of emergent shoots of all sizes. The beetles were not found in shaded sites. Commonly, two or three beetles were found feeding on the same shoot. The beetle remained on a single shoot for one or two nights, and during this period usually ate all the shoot tips. Single beetles required about 30 minutes to eat a shoot tip. They then crawled down the branch and out onto another branch to another shoot tip. *P. punctulata* ate 5-60 percent of the shoot tips that were destroyed by insects during the first part of the rainy season in the control subplots (Jun. and Jul., 1964). Once the beetles had removed the shoot tips from all of the plants in a small area (e.g., one-fourth acre), they left and a new crop of shoot tips developed.

P. punctulata ignored the attack of *P. ferruginea*. Very commonly there were up to 100 workers attacking a single beetle while it fed. The only time the beetle appeared to notice was when stung under the labrum. Then the beetle brushed off the ant with a foreleg. The beetles were rarely found on unoccupied shoots because unoccupied shoots usually lacked undamaged and succulent shoot tips, and the adults did not remain long on such shoots.

Diplotaxis denigrata Bates.

Diplotaxis denigrata is an 8 mm long dark brown melolonthine scarab. From late May through the first week in August the adult beetles were commonly found feeding at night on *Acacia macracantha, Acacia chiapensis* and on unoccupied shoots of *A. cornigera*. They ate the shoot tips and new leaves, and flew to the plants shortly after sunset. While up to 1,000 individuals were counted on one shoot *of A. macracantha,* the number on *A. cornigera* ranged from 1-50. When there were over 10 bettles on a shoot, they usually destroyed every new shoot tip in one evening of feeding. In the area where the beetles were very common (plot M and L) they were rarely found on shoots lacking undamaged shoot tips, but if a dying plant had as few as one shoot tip remaining, it often had *D. denigrata* adults feeding on it.

Adults alighting on shoots occupied by *P. ferruginea* were attacked immediately and they dropped off or flew away. On one occasion, a series of heavily occupied shoots of *A. cornigera* had shoot tips eaten by *D. denigrata* because the evening was too cool for the ants to be active outside of the thorns without substantial disturbance of the colony. The beetles did not provide this disturbance. Feeding *D. denigrata* did not shake the foliage to any noticeable degree.

One specimen of *Diplotaxis simplex* Bates was also taken while feeding on *A. cornigera* along with a large group of *D. denigrata*.

Anomoea sp.

Anomoea sp. probably *A. rufifrons* is a 1 cm long clytrine chrysomelid with yellow males, and black females with a red thorax and a broad red elytral band. The adults were present from late May through late August and were most abundant in June. They fed during the day on undamaged shoot tips and rested at night on the ends of lateral branches. *A. ?rufifrons* was a voracious feeder and concentrated on the tips of the shoot tips. One male was observed to eat the terminal 1 cm of a shoot tip in 16 minutes. Adults of both sexes were found feeding on *A. chiapensis* as well as on *A. cornigera*. Normally, *A. ?rufifrons* was found more commonly on *A. chiapensis* but it became very common on the *A. cornigera* in the experimental plots that lacked *P. ferruginea*. This beetle was the most desrtuctive of the species of clytrine chrysomelids that fed on unoccupied *A. cornigera*. Its importance was accentuated because it was active during the major part of the growing sesaon (rainy season) and was very adept at finding unoccupied shoots that still had undamaged shoot tips.

The adult beetle was very sensitive to the approach of worker ants and usually flew from the shoot before the approaching ant could contact it. If a worker did catch the beetle, the beetle usually fell to the ground and eventually dislodged the ant. When the beetle flew from the shoot, it did not return to the same plant but flew on until it found another. A female was observed to land on 11 different occupied shoots in 3 minutes and 14 seconds and was chased from each one by *P. ferruginea*.

Chrysobothris sp.

Chrysobothris sp. near *C. multistigmosa* is a 25 mm long, brown buprestid beetle. The adults were common throughout the year on *A. cornigera* and *A. chiapensis*. They flew readily between the shoots and rested on unoccupied shoots at night. They were occasionally seen eating the midribs of leaves and pinnae. The females oviposited in freshly cut stumps and shoots, and in dying shoots that were still standing. The larvae were occasionally found to kill shoots with a 1.5-3 cm basal diameter by internal girdling. They were a very common cause of mortality to unoccupied living stumps of both *A. cornigera* and *A. chiapensis*.

The adults walked with a quick, jerky pace that attracted the patrolling and cleaning workers on occupied shoots. Usually, a single ant attack was sufficient to cause the beetle to fly from the shoot; it then flew directly to another shoot. The larvae were unaffected by the presence of the ants since they are under the bark.

Acanthoscelides oblongoguttatus Fahr.

Acanthoscelides oblongoguttatus is a 6 mm long, mottled brown bruchid beetle. Associated with the fact that there was a small percentage of shoots with seed pods present throughout the year, adult beetles were likewise present throughout the year. They were also occasionally seen on the foliage and at the foliar nectaries of *A. cornigera*. This bruchid was reared only from *A. cornigera* and *A. sphaerocephala* in this study. The larvae of the few females that found the seed-bearing shoots at the time when the pods were still green but the seeds were blackening, achieved 5-75 percent destruction of the seed crop. Those females that arrived later and the ones of the first generation offspring completed the infestation of the remaining seeds. The mature pods usually remained on the shoots long enough for at least two generations of beetles to pass through them (2-3 months). The only seeds that survived were those that were carried from the shoot by birds or fell to the ground after birds opened the pods, and were not infested before leaving the shoot.

Adults of *A. oblongoguttatus* were most active on the pods in the late afternoon. The worker ants that were patrolling the pods attacked them whenever they were encountered but the beetles just flew to another pod. Since the worker ants did not bore into the pods and the beetle larvae were inside of the seeds, the ants had little or no effect on the larval bruchid infestation. Once the adults had emerged through their exit hole, the ants did not enter the pods but other insects did.

Coxina hadenoides Guen.

Coxina hadenoides is a very common noctuid moth with a 15 mm wingspread. The forewings are finely mottled brown, white and black, and the hindwings cream with slight dark markings. The mature larvae are about 3 cm long and 4-5 mm in diameter. They may be yellow, gray, or brown and are characterized by two large black spots on the ventral side of the abdomen. When resting during the daytime, a larva holds itself appressed to a branch or else straight out from the branch at an acute angle while holding on with just the prolegs and looks like a dead twig. The first instar and older larvae were found at night feeding on the shoot tips of *A. cornigera, A. chiapensis* and rarely on *A. macracantha*. Mature foliage was not eaten except when the larvae were starved. During the day, the larvae rested upon unoccupied shoots. If the shoot was occupied, they usually walked off onto other plants. The cocoon was spun in the leaf litter on the ground. The moths and larvae were present in the field throughout the year.

C. hadenoides did more damage to *A. cornigera* in the Temascal area than did any other species of insect. The larvae wandered from shoot to shoot, and a third instar larva could eat 3 to 6 shoot tips in one night. The larvae fed unhindered on unoccupied shoots. The degree of damage inflicted by *C. hadenoides* to occupied shoots was a function of the density of patrolling and cleaning workers at night. If the attack of the workers was sufficiently strong as a larva started onto a shoot, it turned around and left. This required more than an occasional worker. Each worker that bit the larva was grabbed with the mandibles and forelegs and thrown from the shoot by the larva. An attack frequency of about two workers per second for more than 2-3 seconds caused a larva to leave. If the workers came in waves, a larva could remove up to four per second.

If not deterred when first climbing onto the shoot, the larvae walked to the top of the shoot. If undamaged shoot tips were found, the larvae began to feed almost immediately. The workers cleaning and patrolling in the area of the shoot tip usually attacked immediately and were thrown from the shoot. If the frequency of attack was high enough (about 2 workers per second) a larva would run down onto a thorn or leaf and take up a resting or defensive position. In the latter case, the larva backed out onto the thorn, with its head toward the branch and held about 5 mm above the surface. The attacking workers usually contacted the larva just anterior to the first pair of prolegs and were easily grasped and removed.

On 3 July 1964, a last instar larva that was placed on an occupied shoot at 9:00 a.m., was backed into a defense position on a type A thorn on a lateral shoot. In 32 minutes, it threw 75 workers off of the shoot. If the evening became cooler and worker activity outside of the thorns decreased, the resting larvae moved back to the shoot tip to feed. As many as seven larvae were found on the single shoots that normally had a large worker force outside of the thorns but for some reason did not on that particular night.

First and second instar larvae were not strong enough to throw ants off of them but they ran (looped) almost as fast as the workers. When chased off the shoot, the larvae often dropped a few centimeters on a silk thread and later climbed back up to the leaf. The only shoots that went through an entire growing season without being damaged at least occasionally by *C. hadenoides* were regenerating suckers from large stumps which were occupied by a very large queen-unit which had moved in from the canopy of the cut shoot.

On one occasion, a worker was observed to bite a larva of *C. hadenoides* behind the head in such a manner that the larva could not grab the worker. However, each time the worker brought her gaster around to sting, the larva bit the gaster and the worker retracted. After about 15 minutes of this struggle, the author picked up the larva . The larva regurgitated a clear fluid onto the author's fingers. Some of this contacted the worker and she was completely paralyzed in less than 5 seconds.

Syssphinx mexicana Bsdv.

Syssphinx mexicana is a yellow syssphingid moth with 5 cm wingspread. The larva is green with silver and red markings; when fully mature it is three inches long and 1.5 cm in diameter. Both adults and larvae were present from late May through September. The eggs were glued in rows of 2-5 eggs on a leaf midrib, thorn or branch. Egg parasites were found in one egg clutch. The eggs required 6 days to hatch and the larvae matured in about 20 days. Starved larvae pupated when about one half normal size and produced apparently normal but smaller adults. The larvae burrowed into the surface litter to pupate. Out of 51 last instar larvae collected in the last two weeks of July, 28 were parasitized by 1-4 large tachinid larvae. Five larvae consumed essentially the entire crop of mature leaves of a 200 cm tall shoot (approximately 200 leaves) during their maturation.

When ovipositing, the female was attacked by any workers of *P. ferruginea* that were present. She hung on the branch or thorn and curled her abdomen up to lay the eggs on the upperside of her support. The abdomen and legs are covered with a dense yellow pile. When the workers bit her, they only succeeded in pulling out a tuft of this pile. Workers found the moth's abdomen difficult to walk on and fell off frequently. It took the female about five seconds to lay five eggs. On a shoot with many active workers, about five workers attacked her while she was ovipositing on a lateral branch. More than six larvae or eggs were not found on a single occupied shoot. The adult female usually flew 3 to 15 m between ovipositings. She did not oviposit on plants that where below the level of the canopy. The eggs were bitten but undamaged by the workers but they did not persist in this attack. When eggs were found on the shoot that were present for a day or so, there were no workers chewing on them. However, once the larva had hatched and the smooth hard chorion was broken, the workers gradually chewed away the remaining chorion.

It is not known to what extent the newly emerged larvae were attacked by workers. By the time the larvae had reached a length of 3 cm they were not attacked by the workers patrolling the cleaning around them. Larvae were only found on the mature leaves and confined their feeding to them. They fed at night and usually rested on the underside of the leaves during the day. When a shoot was stripped of its leaves, the larvae occasionally tried to feed on the shoot tips. When they crawled up onto the shoot tips, they were attacked by any workers present and usually driven off and back down the stem. By the time the shoot had lost its leaves, the larvae were usually large enough to pupate and they left the shoot. After the shoot was defoilated and the larvae had left, it immediately put out a new set of leaves from the thorn axils.

If a larva was taken from a shoot occupied by one colony and placed on a shoot occupied by another colony, it was usually attacked. It reacted to this attack by smearing regurgitate on the biting and stinging worker. Workers often ran down the body of a larva on their own shoot as if the larva was part of the plant. Even when the larva was eating foliage, workers were observed to run across the chewing mandibles and to completely ignore the damaged area.

It appeared that the attack of the workers affected the number of eggs laid by the female. She normally oviposited her small egg clutches on occupied shoots since these were by far the most common ones. However, it was common to find clutches of 10-45 eggs laid on 3-4 different branches of an unoccupied shoot in an experimental plot (E-1). After these larvae hatched, they very quickly removed the leaves (already in reduced number) and began to wander in the plot. Some found other unoccupied shoots and completed their development.

Clutches of four or five empty egg shells were often found on shoots that had one or two maturing larvae. Predators were almost never observed on occupied shoots except for *Polistes* which did not forage intensively on occupied shoots, apparently due to the constant attack of the wasps by worker ants. A certain percentage of the first instar larvae may have been removed by the workers before the larvae became accepted by the colony.

The females did not appear to fly up to the canopies to oviposit on shoots that were over 3 m tall. About 2 out of each 100 shoots had larvae of *S. mexicana* on them. Though loss of mature leaves was very high, it appeared to have little effect on the plant since the shoot tips were not destroyed, the larvae left and did not continue to eat the new foliage, and the shoot produced a new set of leaves within two weeks.

Aristotelia corallina Wals.

Aristotelia corallina is a gelichiid moth with a 1 cm wingspread and pink, yellow and black markings. The mature larva is 10-12 mm long with the anterior one-half of the body ringed with black and white and the posterior one-half striped with black and white. Adults and larvae were present throughout the year but were most abundant during the last three months of the dry season. During these months, the larvae were very common; in plot J almost every shoot had one to four larval webs spun among the leaves. The larval webs were spun in the tops of shoots within the 10-50 cm size range, and during the night the larva left its web to feed on the shoot tip. The larvae of *A. corallina* were in large part responsible for the lack of height increment of shoots in this size range. During the rainy season the webbing became soaked and this was associated with high mortality among the larvae. At this time, larvae were occasionally found in the tops of taller shoots.

When a colony of *P. ferruginea* invaded a shoot with the larvae and webbing of *A. corallina* on it, within a matter of a day or less, all webbing and larvae were removed. On two occasions the workers caught a larva and tore it into pieces, some of which were carried into the thorns.

Halisidota sp.

Halisidota sp. probably *H. pura* is an arctiid moth with a 2.5 cm wingspread. It has yellow and brown forewings and cream colored hindwings. The larva is densely covered with long yellow hairs. The larvae were common from September through November. They ate the new green thorns on the shoot tips of unoccupied shoots (Fig. 29). While they did not appear to seek the terminal point of the shoot tip, the last 1 cm was usually eaten along with the last green thorn. During the fall growing season, the larvae were responsible for at least 10 percent of the damaged shoot tips in plot L. They fed at night.

Larvae of this moth placed on occupied shoots were immediately attacked by the workers. They bit at the hairs and legs. The larvae tried to escape by running down the leaf or branch and the workers chased them until they ran off the end of a leaf or branch or were forced to let go and fall. Many of the long hairs were pulled out during this harassment but the workers could not get close enough to the body to bite the larva unless they came in from underneath and bit a proleg. The larvae regurgitated on workers that were biting them. This regurgitate did not kill the workers and often did not cause them to let go.

Rosema dentifera Draudt.

Rosema dentifera is a notodontid moth with a 2.5 cm wingspread. The forewings are bright green and cream colored hindwings. The mature naked larva is about 3 cm long and green with widely spaced thin black and white bars. The larvae were common from late July through December and fed on the mature foliage of *A. cornigera* at night. They were found only on shoots with a large worker force. The thin cocoon was spun in the axil of one of the lower thorns, usually incorporating a section of a leaf into the cocoon wall.

The workers cleaned and patrolled around the resting and feeding larvae without disturbing them. They likewise showed no reaction to the presence of the workers. However, if a larva was removed from a shoot occupied by one colony and placed on a shoot occupied by another colony, it was usually attacked immediately in the same manner as were most lepidopterous larvae. The larvae took evasive action by running out onto the end of a thorn and if too many ants followed, they jumped off. Lacking long hairs, they were very vulnerable to the workers. *R. dentifera* was never found on a part of the shoot that was heavily patrolled such as a major shoot tip. It may be that the ants did not tolerate their presence in this area just as they did not tolterate *Syssphinx mexicana* larvae on the shoot tips.

Acromyrmex octospinosus Reich

Acromyrmex octospinosus is a 5-10 mm long red attine (leaf-cutter) ant that was common in the area. On three occasions, foraging columns were observed to remove the shoot tips, green thorns and most of the mature leaves from a young unoccupied sucker regenerating from cut stumps in subplot A-1 and H-1. Their damage was not found on unoccupied and occupied shoots that were over 100 cm tall.

When a queen-shoot was cut and placed against the base of a stump that was being stripped by *A. octospinosus*, the workers of *P. ferruginea* that ran out onto the shoots attacked the leaf-cutter workers immediately. These later workers either ran or fell off the shoot and the trail to the shoot was not maintained.

BIONOMICS OF *PSEUDOMYRMEX FERRUGINEA* F. SMITH

MATERIALS AND METHODS

Collecting colonies. A unique feature of ants that have an obligate relationship with a plant is that the entire colony can be collected as a unit, killed, and later examined without having seriously damaged the distribution of brood within the colony. The ants occupying a shoot less than 100 cm long can best be collected by cutting the shoot into sections and dropping the pieces into a large cyanide jar. The workers of very young colonies often can be induced to enter the thorns by tapping the shoot trunk two or three times. This reduces the loss of workers when the shoot is collected. If large numbers of workers are active on the surface of such a small shoot, they can be easily aspirated from the surface. Except for the few knocked off by the blow, cutting a shoot does not cause the ants to leave and thus the shoot can be transported to a more convenient site for working. The ideal time to collect a large colony is on a cool day (less than 21° C.). At this time, a very low disturbance reaction is produced as the thorns are stripped from the tree.

If it is necessary to collect a large unit on a hot day, the best method is to strip the thorns off one at a time and drop them into a large jar in which a small strong cyanide jar has been placed. As the thorns are removed, there often is a very strong swarming reaction on the shoot surface. These ants are easily aspirated and the entire shoot content is obtained. When placed in the cyanide jars, most workers die in the thorns and the brood is not thrown out. Thus, when shoot sections or thorns are numbered, the morphology of the colony can be reconstructed. Thorns with brood can be preserved with contents intact by dropping them directly in a liquid preservative. Large colonies were also collected by spreading a sheet under the shoot and spraying the latter with parathion. After several hours had elapsed, and most of the workers outside the thorns had dropped from the shoot, the thorns were stripped off. However, this method is awkward and time consuming.

When collecting samples of workers that are seen doing particular things on the shoot surface, extreme care must be taken not to disturb the colony so that the collection site does not become covered with disturbed workers. If the queen is desired, she is obtained most easily by choosing a large colony on a shoot at least 10 m from any other shoot. The four or five largest clusters of type B thorns are stripped off and each thorn is cut open until one is found packed with eggs. If the queen is not in the egg-filled thorn, she is usually in an adjacent one having an enlarged entrance. If she is in none of these thorns, she has recently moved to another thorn higher in the acacia, or the shoot contains an auxiliary-unit without a queen. Founding queens are easily collected by opening the thorns of 20-50 cm tall shoots that have no workers on them. Alates are most readily obtained throughout the year by opening type A thorns on lateral branches of shoots 3 or more m tall.

Transporting live colonies. Units can be easily transported when in the shoot. A whole shoot is cut and tied to the outside of the car; the wind prevents the ants from leaving the thorns. Shoots with their roots can be dug up and transplanted. The leaves usually fall off but new leaves are produced so rapidly that the colony is not lost through starvation. The occupants of a thorn can be kept inside by plugging the entrance with a piece of wood (a broken off thorn tip is convenient); the workers chew through tape.

Recording ant activity outside of the thorn. The number and distribution of worker ants outside of the thorn is of great importance to the acacia. The most reliable fast counts are obtained using a hand-counter and starting at the base or top of the shoot and moving up or down. After this count on the main trunk, or concomitant with it, those on the lateral branches are counted. When over 50 workers are present of the surface, it is reasonable to count by fives or tens; this method gives about 90 percent accuracy. In making a census of this type, the faster the counts are made the more accurate they are; workers move around on the tree but tend to stay in one general area for 1 to 10 minutes. Only those visible from one side of the shoot can be reasonably counted at one time but since there is much more lateral movement than vertical, a count on one side only takes in 75 to 90 percent of those on the surface. The wider and taller the shoot the less accurate the surface count is but since most experimental plots contained roughly even-aged shoots, comparisons seem valid within the plot. There is no strict relation between the numbers of workers on the shoot surface and the type of unit living in it. In general, the larger the colony the more workers there are on the shoot surface under given environmental conditions, but this is a highly variable parameter.

Marking workers. Individuals can be marked with a small dot of white paint (Testor's Dope) on the thorax or gaster. It is best to apply this with a single horsehair while the worker pauses, since handling them introduces the possibility of injury to the ant.

Mating flights. Once the site of a mating flight of *P. ferruginea* is located it is very simple to observe mating behavior in detail. Mating activity usually continues well into the early daylight hours and can be closely observed by climbing the object around which the swarm is taking place. The presence or absence of an early morning mating flight is easily recorded by hanging a 20 x 20 cm piece of sheet metal covered with sticky tree-banding compound high up on telephone poles or on the fronds of prominent outstanding palms in the area. Both males and females adhere to the surface.

Maintaing laboratory colonies. The reactions of workers to brood and reproductives is best determined by observing laboratory colonies in glass tubing. Large colonies (over 500 workers) can be maintained in the laboratory by feeding them honey and Beltian bodies. The colonies are started by stripping about 30 of the largest thorns off of a 180 cm queen-shoot. These thorns are then chilled in the freezer compartment of a refrigerator until the workers are immobile. The contents of six thorns are then dumped into a 14 by 500 mm glass tube with one end plugged with cotton and a strip of paper toweling within the tube. Five of these tubes are laid at right angles across six 4 by 400 mm glass tubes that are supported 10 inches above a 100 x 50 cm metal sheet. The margins of this sheet are ringed with tree-banding compound. Water moats are unsuccessful since large numbers of workers drown themselves. Honey is dripped on plastic strips laid parallel to the large diameter tubes. To provide Beltian bodies a shoot tip with several mature subtending leaves is placed in a bottle of water of the metal sheet so as to contact the tubes. Any swollen thorns on the shoot tip are clipped. To provide new shoot tips, the 5-10 workers on the wilted shoot tip have to be sacrificed.

The chilled workers revive almost immediately and after a day pile the brood at one site in each of the big tubes. After a period of several days to a week, the queen and her tube's contents are moved by the workers into one of the long 4 mm diameter tubes. Gradually the remainder of the brood is moved into these narrow diameter tubes. For the first week, the colony is given only honey and the queen becomes less physogastric and ceases egg production. When a shoot tip is presented, Beltian body harvest occurs immediately. Within 6 to 12 days the queen regains her physogastric condition and egg laying is resumed. These colonies appear relatively normal and workers patrol the outside of the glass tubes in much the same manner as they patrol a shoot. They collect the major part of the honey just before dawn even though it is available for 24 hours. The queen with her eggs remains roughly segregated from the other brood in one of the narrow tubes but larvae are present in other parts of the same tube. The queen moves around much more than she would have been abel to in a thorn on the shoot.

Founding queens with their first brood and a few workers can be kept temporarily in pill-boxes with cover-slip glass tops. A small vial of honey is placed inside. Groups of workers with brood can also be kept in this manner.

SYSTEMATICS. Substantial confusion has surrounded the taxonomy of the reddish-brown pseudomyrmecine ant discussed at length in this paper. With the exception of the type description (F. Smith, 1877), *Pseudomyrmex ferruginea* has been primarily discussed in the literature as *Pseudomyrmex belti fulvescens* Emery (1890) or *Pseudomyrmex fulvescens* Emery (1890). Emery's type specimen has clearly come from the population discussed in the present paper; F. Smith's type from Mexico (contained in the British Museum) has kindly been compared with representative specimens from eastern Mexico by Dr. I. H. H. Yarrow and there is little doubt that the common reddish-brown obligate acacia-ant in eastern Mexico is *P. ferruginea.*

The rare, smaller and yellower obligate acacia-ant in eastern Mexico is *Pseudomyrmex nigrocincta* Emery (1890); it becomes progressively more abundant along the Pacific lowlands of Central America down to Costa Rica. See Janzen (1967a) for a discussion of the taxonomic problems associated with the obligate acacia-ants in Central America.

A few species of ants besides *P. ferruginea* (Fig. 40) may be found living in dead or live swollen-thorn acacias within the study area. Since these ants do not have the same influence on the ecology of the swollen-thorn acacias as does *P. ferruginea,* these ants are mentioned below so that a shoot inhabitated by them is not recorded as being occupied by *P. ferruginea.* The other two species of *Pseudomyrmex* occasionally found living in live swollen-thorn acacias, *Pseudomyrmex nigrocincta* and *Pseudomyrmex gracilis mexicana* Roger are discussed in the section entitled OTHER ACACIA-ANTS IN THE STUDY AREA. At least three other species of *Pseudomyrmex* may be found on very rare occasions living in thorns opened by other ants; they use these thorns in the same manner as hollow twigs. Ants in the genus *Crematogaster* often live in the thorns of large dead or living unoccupied swollen-thorn acacias. They enter through entrances made by founding queens and workers from previous occupation, and though the holes made by microlepidoptera and zygopine weevils when the adults leave the thorn. These latter holes are usually on the sides of the thorn, or near the base. In the population of *A. sphaerocephala* growing along the dunes south of Veracruz, *Crematogaster* is the usual occupant of the plant. *Crematogaster* is most easily distinguished from *P. ferruginea* by the former's small size (2-4 mm long), petiole attached to the dorsal side of the gaster, heart-shaped gaster, and slow rate of movement. *Camponotus planatus* Roger is occasionally found living in thorns on unoccupied, and more rarely occupied, shoots; it cuts its own entrance holes and/or uses those made by

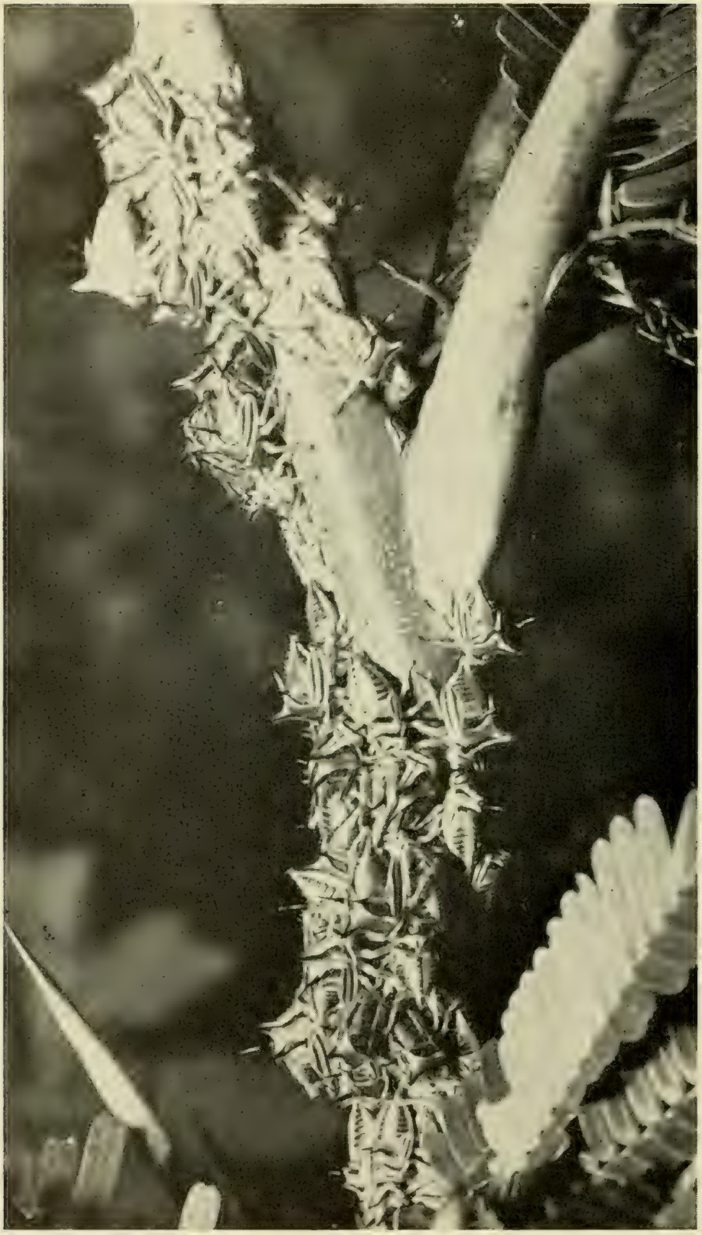


FIG. 28. A brood of nymphs of *Umbonia orozimbo* on an unoccupied 110 cm tall shoot of *Acacia cornigera* in subplot N-1. The adult female is out of sight above the brood. When this stem was placed on an occupied shoot, the workers of *Pseudomyrmex ferruginea* chased the membracids from the shoot. Photo November 1963.

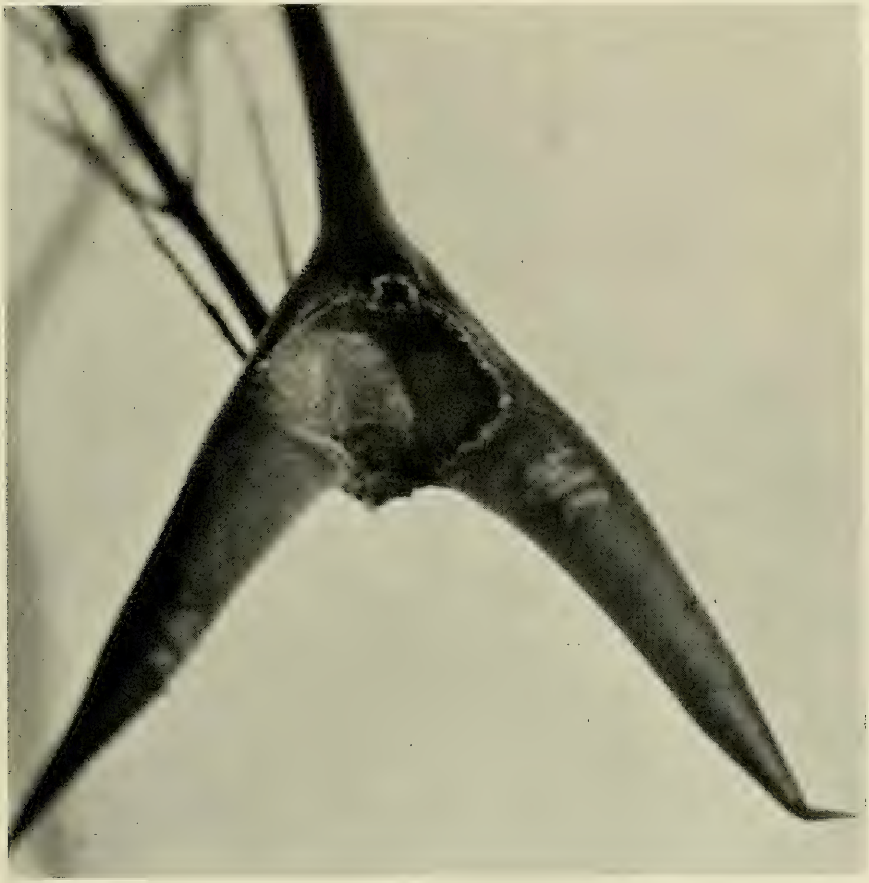


FIG. 29. Thorn and shoot tip damage by the larva of *Halisodota* probably *H. pura*. This was the terminal node of an unoccupied *Acacia cornigera* in subplot J-1 in November 1963. The shoot was 20 cm tall. Mandibular scars can be seen on both sides of the thorn. The feeding damage of tettigoniid grasshoppers is very similar to this.

P. ferruginea. These entrances are larger and rounder than those of *P. ferruginea. C. planatus* is a short, broad ant (4-6 mm long) with a spherical gaster and one petiolar segment (*P. ferruginea* has two petiolar segments). It has a reddish-brown head and/or thorax, and a black gaster.

Distribution. The geographic distribution of *P. ferruginea* in the study area is congruent with the combined ranges of *A. cornigera, A. sphaerocephala,* and *A. chiapensis* (Fig. 6). The ecological distribution of *P. ferruginea* is discussed in the later section entitled ENVIRONMENTAL REQUIREMENTS. Aside from seedlings or suckers less than a year old, single unoccupied shoots of *A. cornigera* and *A. sphaerocephala* are only occasionally encountered. No local populations of these two swollen-thorn acacias are known or reported without colonies of *P. ferruginea,* except for a band of *A. sphaerocephala* about 30-3000 meters wide immediately adjacent to the high-tide line on the ocean beach from a point about 3 miles south of the city of Veracruz, south to Anton Lazardo. Shoots of *A. chiapensis* frequently lack a colonoy of *P. ferruginea.*

P. ferruginea was not collected thorughout the study area, at every site where it was observed. However, enough samples were taken to assure that its distribution shows continuity and discontinuity in the same manner as that of the swollen-thorn acacias. The geographic range of *P. ferruginea,* like that of *A. cornigera,* has apparently not been greatly extended by man's disturbance of the vegetation. However, prior to human destruction of most natural plant communities in the study area, the distributional pattern of *P. ferruginea* was the network of arroyos, rivers, and ocean beaches. Man's activities have filled the lacunae in this network with many acres of highly suitable habitats for *A. cornigera, A. sphaerocephala,* and *P. ferruginea.* Now these two acacias and their ant have a much more continuous distribution.

Morphology of Individuals. *Morphology of immature stages.* When foliar nectar and Beltian bodies are available, the large white cylindrical eggs are laid continually by the single colony queen. They are only very slightly sticky, and clusters of them are easily shaken apart.

Numerous pseudomyrmecine larvae are described by Wheeler and Bailey (1920) and Wheeler and Wheeler (1956). *Pseudomyrmex ferruginea* is treated in both papers under the name *Pseudomyrmex belti* subsp. *fulvescens.* As is the case with most pseudomyrmecine larvae, those of *P. ferruginea* are elongate with well developed dorsal hooked hairs. These hairs serve as anchors to hold the larva in place on the slanting inner walls of the hollow thorns, and on other larvae. The larvae range from 0.7 mm (first instar larvae) to 6.7 mm (larvae that will produce alates) in length. Well fed larvae are nearly circular in cross section, but under starvation conditions a deep longitudinal ventral depression develops; at this time the larva becomes shorter and much of the visible white fat body disappears. The inactive prepupa is easily distinguishable from the larva by the former's lack of dark gut contents. The pupae are not enclosed in a cocoon. Development from newly laid egg to freshly emerged worker takes about 35 days during the dry season and rainy season. Since the larvae can live at least a month without food, shortage of food undoubtedly lengthens this time of development.

Morphology of worker. Form. *P. ferruginea* is a representative, medium sized pseudomyrmecine. The worker has short legs and an elongate body that is held low to the substrate. The large convex compound eye covers about one-half of the side of the head. The ocelli are well developed. The head is wider than the thorax and bears short mandibles with 3-4 teeth. The two petiolar segments are sufficiently flexible to allow the sting to be brought to bear on any point touching the worker. The small, tear-drop shaped gaster is carried straight out to the rear.

Dimensions. While there are distinct behavioral roles within the colony, the workers display monophasic allometry in respect to head width contrasted with thorax width (terminology of Wilson, 1953). From Figure 30 it can be seen that there may be considerable variation in thorax width for a given head width but there is no indication in any of the colonies examined of polyphasic allometry or dimorphism among the workers.

There are obvious size differences among the workers of colonies of all ages. Workers range from 3.5-7.0 mm in length. The workers produced

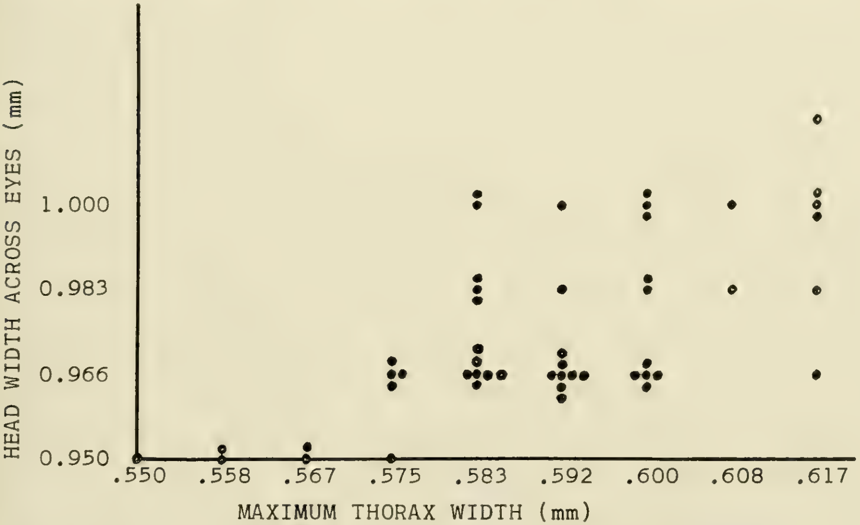


Fig. 30. Head width across the eyes plotted against the maximum thorax width of 50 workers of *Pseudomyrmex ferruginea* from a one year old colony. There is no indication of polymorphism or strong allometry in respect to these two measurements. The relationship is likewise not linear. Sample from a 2,000 worker colony from *Acacia cornigera* 1 km west of Temascal.

by a colony living in a young shoot become progressively larger until the colony is about two years old. This change may be in part due to the increasing amount of food that is generally available to the colony as it grows. It is also associated with the increasing efficiency of older workers to harvest food. In figure 31, the head widths of workers (A: $\overline{X}$=1.002 mm, s.d.=0.0026) from a relatively young colony (345 workers) and the head widths of 345 workers (B: $\overline{X}$=1.084 mm, s.d.=0.035) from a three year old colony are plotted (about 5,000 workers). Measurements of other colonies indicate that these two histograms may be regarded as two successive stages in the development of worker size in a colony, with (B) being close to the maximum. The workers representative of the size and age class in the first histogram (A) have probably all died in the colony from which the second sample was drawn (B). However, this latter colony still is producing an occasional worker in the size class represented by histogram (A) in Figure 31. The significance of this to an occupied shoot is that not only do older colonies have more aggressive workers, but they have larger workers as well.

Variation in color. Throughout the study area, the gaster of *P. ferruginea* varies from reddish-yellow to black, but teneral workers require about three weeks to be completely darkened. Other body parts range from yellow to dark brown. In the Temascal area, the integument of the teneral worker is pale yellow to beige at the places where it will be reddish-brown when fully tanned. It is purple-gray where it will be black. The two most common color phases are some shade of light reddish-brown with slight or no darkening of the gaster, and some shade of reddish-brown with a very dark brown gaster. These are found throughout the study area. All intergrades of these two patterns may occur in one colony but usually the colony conforms to one color phase or the other. Colonies with very dark workers are found scattered throughout the study area (most commonly around Veracruz and Tampico). In the Temascal area there were several colonies with almost yellow workers. By far the commonest color phase is that with the dark gaster. There is no evidence that these color patterns represent sibling species.

Temporary variation in form. When collecting nectar, a worker visits many successive foliar nectaries. The gaster sometimes enlarges as much as three times the usual volume and the sclerites become separated like those of a physogastric queen. When a worker is confined without fluids for a period of two or more days, the volume of the gaster drops to about one-half that usually observed.

Morphology of alates. Female. The alate female does not differ from the worker in form except in the longer head, two times larger ocelli, greater body size, and thorax modified for flying. While larger than the workers, alate females are much less variable in size. They range from 7.7-8.2

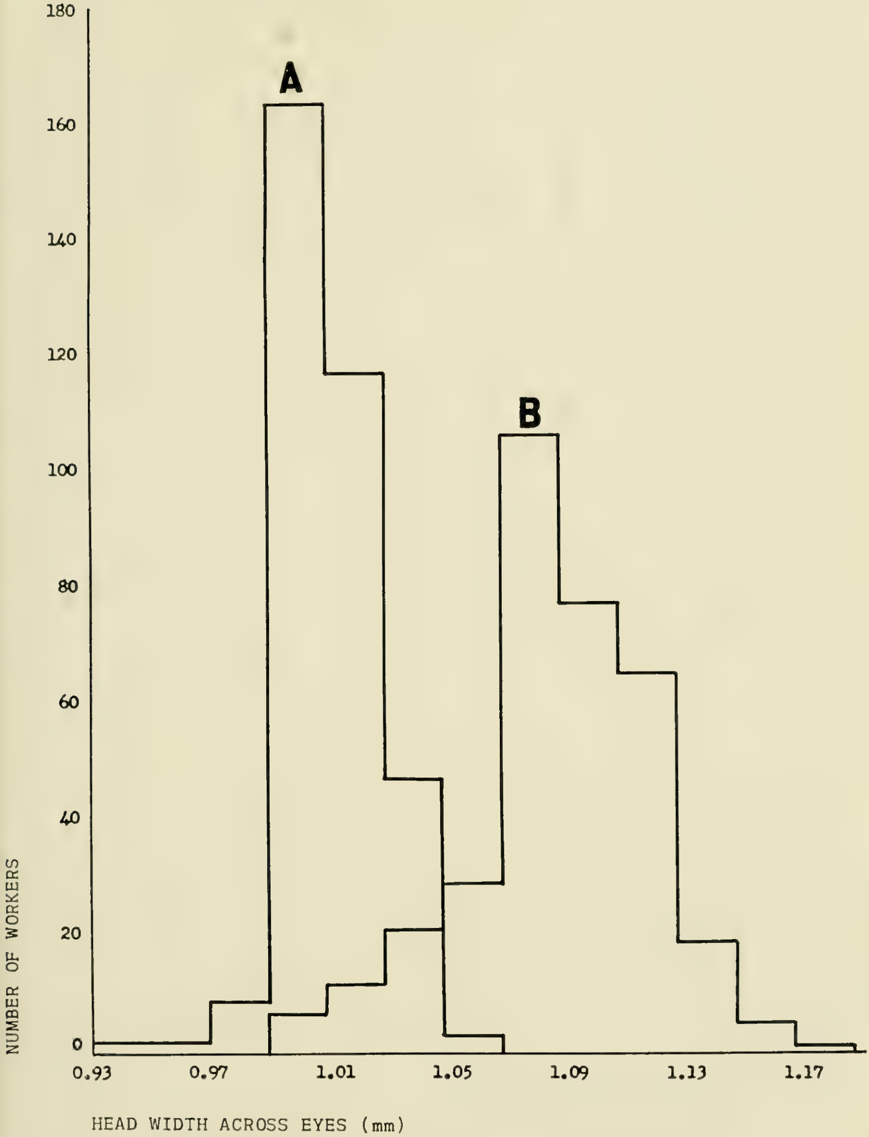


Fig. 31. Frequency distribution histogram A is the head widths across the eyes of all the members of a 345 worker colony of *P. ferruginea.* This colony was about one year old. Histogram B is the head widths across the eyes of a sample of 345 workers from a colony about three years old with about 5,000 workers. Both colonies were collected from *Acacia cornigera* about 7 km east of Temascal.

mm in total length (sum of mandibles, head, thorax, petiole, postpetiole, and gaster).

The color changes that take place as the teneral worker ages are the same as those described for the worker. The alate females have the same color phases that the workers do. Usually the color phase of the queen of a colony matches that of the workers and alate females in the colony, but on two occasions a queen with a pale gaster was found with workers with dark gasters.

When a founding queen is gathering nectar from the foliar nectaries, her gaster increases to about twice the usual volume. The gaster of a fully physogastric queen may be as large as 7 mm long and 3-4 mm wide. In this case, the sclerites are about 0.75 mm apart. The normal dimensions of a founding queen's gaster are about 2.5 mm long by 1.5 mm wide. Under starvation conditions, the colony queen's gaster returns to nearly normal size within two weeks.

Male. The males are representative, medium sized pseudomyrmecines (7.9-8.2 mm long, including mandibles). Like the alate females, they vary little in size. The compound eye is very large and protruberant, covering nearly one-half of the side of the head. The ocelli are very prominent (0.15 mm in diameter); this development is very likely associated with the mating flight which begins before dawn.

COLONY MORPHOLOGY AND DEVELOPMENT. *Structure of colonies in single shoots.* A *Pseudomyrmex ferruginea* colony is initiated when a dealate queen opens an acacia thorn for her own use, or occupies a thorn opened by an earlier worker or founding queen. This occurs at all times of the year. From this single thorn the colony grows to occupy, either by use for brood or by patrolling, all of the thorns on the shoot. Under the proper circumstances, the colony also spreads to other shoots of swollen-thorn acacias. Thus, the mature colony lives in and on a series of dispersed containers (thorns) with exposed routes connecting them (branches of the shoot or trails between shoots). Since a colony confined to one shoot has a different structure from one living in several shoots, the former condition is discussed separately from the latter. The variation in colony structure is primarily a function of shoot age and form, colony age and history, and time of year.

Location of the queen. The shoot in which the founding queen settles may have from one to at least 2,400 thorns. In younger shoots (1-200 thorns) she is alone or shares the shoot with as many as 34 other founding queens that have colonies in various stages of development. In a shoot that lacks an active worker force, the founding queens may be in almost any thorn with at least one side over 15 mm long. On 23 Jul. 1964 the 90 thorns on 29 shoots in subplot J-1 contained 14 founding queens without any brood, 23 founding queens with eggs only, 28 founding queens with eggs and larvae, 10 founding queens with eggs, larvae and pupae, and one founding queen with eggs, larvae, pupae and three workers. There were 2 thorns with more than one founding queen and each of these thorns had two entrance holes. All thorns were under 90 days old. Of the 16 remaining thorns, 5 had no entrance, 3 were damaged or rotten, 2 had dead queens, 3 were empty, 1 had a salticid spider web, and 1 harbored a colony of a small yellow *Solenopsis.* The maximum age of these thorns is known because all thorns were clipped from these shoots on 25 Apr. 1964. The shoots had a mean height of 28 cm (s.d.=9 cm) and were among herbaceous and woody sucker regeneration in a fallow corn field.

In large unoccupied shoots having over 200 thorns, founding queens tend to be in the type A thorns on lateral branches. Damaged or old rotting thorns are usually only tenanted by queens that are hiding and usually when all other thorns are tenanted. There is no indication that thorn size influences the probability of the founding queen, becoming the queen whose colony eventually controls the entire shoot, and destroys the other incipient colonies.

Isolated sucker shoots over a year old and seedlings over two years old (often over 100 thorns) usually contain a queen-unit. The consequence is a reduction, often to zero, in the number of founding queens present. In such a shoot, the few founding queens present are found in rotting thorns, or thorns very marginal to the general area of thorns, leaves and growing points. The number of founding queens in other parts of a shoot reflect the size, age and type of unit, i.e., whether a queen-unit or auxiliary-unit.

During the latter part of the dry season (Mar.-May) and during the cool season (Dec.-Feb.) there is a reduction in the number of searching queens in the field with a consequent reduction in the number of founding queens in the thorns. Even so, on the average there is still more than one founding queen per regenerating shoot. This reduced number could increase production of incipient colonies since it could lower competition among founding queens for thorns, Beltian bodies and nectar. On the other hand, there is high mortality among the small colonies that have only eggs and larvae. If this is due to some inherent physiological cause, such that it is necessary to have many queens starting to get a few maturing colonies, then the periods following the cold and dry weather might be expected to show a lowering in production of mature colonies. In fact, the rate of colony production at this time is not lowered.

Until there are 15-20 workers, the queen stays in the same thorn with all of her brood and most of the workers. However, she may move with all of her colony members to a new thorn. On 27 May 1964, 21 sucker shoots with a mean height of 33 cm (s.d.=23 cm) were dissected. The surrounding vegetation was 100-150 cm tall and was completely burned on 1 Dec. 1963. On 13 Jan. 1964, only 66 of the 142 thorns on these new shoots had founding queens in them. During September, there would have been greater than 95 percent occupation by founding queens. In May, the dissected shoots had 210 thorns with no entrance holes; 83 empty thorns with no founding queen; 23 thorns, each with a founding queen and eggs (138 eggs); 10 thorns, each with a founding queen, eggs, and larvae; 3 thorns, each with a founding queen, eggs, larvae, and pupae; 55 thorns, each with a founding queen, eggs, larvae, pupae and workers(mean number of workers per thorn was 3.7, s.d.=3.1); and 2 thorns occupied by one small expanding colony (12 workers). The largest colony had 16 workers and had a maximum age of 163 days.

The founding queen can not stay in the same thorn throughout the life of the colony. By the time a queen has produced 10-40 workers, her gastric sclerites begin to separate. By the time she has 100-300 workers she is usually completely physogastric. At some undetermined time she moves into one of the largest thorns on the shoot, usually an undamaged, 1-6 months old type B thorn. This thorn is roughly in the center of the present year's thorn and leaf mass. As the location of the thorn mass moves upward with the growth of the tree, she changes thorns at least 1-3 times per year. She therefore remains roughly in the center of the thorn mass in one of the largest thorns.

Placement of brood. In the early stages of colony development, most of the brood is located in the same thorn as the queen. Founding queens are usually accompanied by 4-15 eggs before the first larvae are present. These eggs are usually scattered separately in the lowest part of the thorn. During the first 2-9 months of shoot regeneration in an area completely cleared of old colonies, queens with only eggs, or with eggs and a few larvae, are most commonly encountered. As more members are added to the colony, it remains in the original thorn until it is packed with brood and adults. Egg production remains low at this time; this first thorn usually contains less than 50 eggs.

As the worker force grows, control of new thorns is gained (e.g. 1 thorn, 11 workers; 2 thorns, 19 workers; 5 thorns, 55 workers; 13 thorns, 125 workers). As the number of workers in the colony increases, the percentage of thorns used for brood decreases to a level of about 50 percent. This percentage is highest during periods of shoot growth activity which is highest in the rainy season and lowest toward the end of the dry season. At the end of the dry season, entire trees may be abandoned. This low use of thorn space is in part associated with the unsuitable nature of some thorns for the brood. It is also associated with a lack of food. About 50 percent of the leaves produced are subtended by swollen thorns. If the Beltian bodies produced by the four leaves associated with 2 swollen thorns are only sufficient to support the larvae of one thorn until four more leaves are produced, then only about 50 percent of the thorns available to the colony can contain brood (based on the fact that only 50 percent of the leaves have swollen thorns). It is probable that the number of Beltian bodies produced by two leaves is not sufficient to nourish a thorn full of brood to the adult stage. Even when there is a surplus of Beltian bodies the colony is not able to grow fast enough to use all of the old thorns and the new thorns that are produced with the new leaves. On this basis, a colony provided with the products of a single shoot could never fill all the thorns of one year with brood, especially since it has last year's thorns to fill as well.

The number of larvae in a brood thorn is variable. The upper limit of brood dispersion among the brood-thorns is probably a function of worker efficiency. On any given shoot, the number and volume of brood in a thorn is only roughly proportional to the size of the thorn. As the proportion of later instar larvae in a thorn increases, the number of larvae in the thorn decreases.

When the colony is first expanding, the worker force occupies those thorns that it can and uses them for brood. These are often, but not necessarily, adjacent to the thorn occupied by the queen. Relatively soon, when the colony has 4-8 thorns and 40-100 workers, new green thorns are occupied as they appear. As control of the entire shoot is achieved by destruction of competing colonies, the brood-thorns are chosen so that the brood is concentrated roughly in the center of the mass of thorns and the degree of expansion from this center is a function of the amount of brood. Colonies five or more years old often have the brood-thorn area fragmented into clusters that are spread throughout the canopy and are located closer to the major areas of new leaf production than to the center of the canopy.

The area of thorns with brood is effected by the dynamics of *A. cornigera.* As the area of 1-2 year old thorns moves upward with growth of the shoot, so does the area of brood thorns. This area roughly conforms in shape to the shape of the canopy of the shoot. This is one way in which the colony structure can be influenced by the surrounding vegetation. Slender shoots have long, thin brood areas, while spreading shoots have laterally extended brood areas.

Within the brood area there are occasional empty thorns. These often are green, damaged (thorn cavity opened), or strongly distorted (only one side of the thorn swollen). These thorns rarely lack entrance holes. The number of empty thorns in the brood area increases and the brood area becomes smaller as 1) the colony becomes senescent in old shoots, 2) the growth rate of the colony decreases due to lack of food during the cool and dry season, or 3) the number of thorns produced increases without concomitant colony size increase. The number of thorns available to the colony increases during the first 3-4 years of colony growth and then decreases.

The number of immature individuals in a colony increases from year to year. In a shoot old enough to react to the cool or dry season by reduction in growth rate, the rate of increase in larvae is highest during the first six months of the rainy season and slows to zero only with cessation of all new leaf production during the cool or dry season. Except when starving, the colony always has eggs present. The rate of egg production approaches zero when the queen moves to a new thorn but is re-established immediately following her settlement in a new thorn. With the exception of eggs, there is no segregation of the immature forms between thorns. There is a suggestion that the new first instar larvae (or eggs) are brought to the brood thorn in even-aged groups but during their growth are reshuffled through the thorns and unevenly fed. This results in the thorough mixture of instars and sizes found in most brood thorns. Green to tan thorns that are less than two weeks old are often found with all larval ages, sexes, and castes in them.

The eggs are partially segregated from other brood. Except when the physogastric queen has recently moved into a new thorn, she is accompanied by 400-800 eggs, 0-70 first instar larvae, and 0-10 later instar larvae. Pupae are normally absent from the thorn with the queen in it. This quantity of brood occupies about 1.2 cc or 60 percent of the volume of the thorn with the queen in it. The eggs are not clustered but adhere very lightly to each other and can be shaken apart. Other eggs in the colony are found in three places. Small groups of 5-40 are occasionally found in brood thorns with first and later instar larvae. These eggs apparently represent a new cohort ready to begin growth in the thorn. Commonly the thorn next to that of the queen is as full of eggs as is the one with the queen. These eggs are occasionally accompanied by small numbers of larvae of all instars and pupae. Occasionally a large thorn full of eggs is found 20-60 cm below that occupied by the queen. This thorn is in various stages of being filled with the normal large numbers of larvae and pupae. It has an enlarged entrance and is the thorn previously occupied by the queen.

Alate brood appears during the second year of colony growth and is mixed with worker brood. Brood of both sexes may be found in the same thorn. The larvae of the first alate forms appear in the margins of the brood-thorn area (type A thorns near the ends of lateral branches). During the third year of colony growth, alates are found in progressively higher numbers and closer to the central area of brood thorns. After the third year, alate last instar larvae and pupae may be found in almost any brood-thorn except the queen-thorns. Alates are often the last adults to be produced by a dying colony or fraction of a colony. Contrary to the usual case with temperate ants, alate brood is present all year.

Distribution of the worker force. Worker numbers increase throughout the year, if Beltian bodies and nectar are available and diurnal temperatures stay above the 24-27° C. level. Increase in worker numbers during the cool and dry season is probably insignificant in comparison to that when large numbers of Beltian bodies are available during the rainy season. The leaves of the flowering branches that are produced during the later part of the dry season bear enough Beltian bodies to cause a small increase in worker numbers. A colony occupying sucker regeneration less than six months old is likely to have sufficient food for growth because shoots of this age from large stumps continue to grow during the dry season. The size of a colony is more strongly associated with the number of growing seasons passed than its age in months.

In determining the number and distribution of workers in a colony, very young colonies may present some difficulty. Usually a shoot with numerous small colonies has one larger colony occupying several thorns and several small colonies occupying only one thorn each. A representative shoot might have 16 thorns: three empty, five with founding queens and only eggs, five with founding queens with eggs, larvae and one to five workers, and three that are packed with brood and workers. Two of the last three thorns would lack a queen and one would have a partly physogastric queen. In this example, the six colonies would have 1, 2, 2, 2, 5, and 31 workers, respectively. Almost all of the workers found outside of the thorns would belong to the last colony.

A shoot with a colony of 200-400 workers, or more, is cleaned of other small colonies by the worker force; counting the workers is therefore no problem. From these low levels, the colony may increase to as high as 12,269 workers in 930 days. This colony was an exceptionally rapidly growing colony in that its shoot appeared to have continued to grow throughout each dry season and therefore the colony grew as well. A more representative colony of this age would have 4000-8000 workers. The actual number of workers produced by the large colony during the 930 days undoubtedly was much higher. A correlation between shoot size or age, and number of workers is only found where a colony occupies a single shoot. The opportunity for the colony to disperse and occupy shoots with different histories destroys this correlation.

In using the age of a sucker shoot to determine the possible age of the colony, care must be taken to use shoots that are growing in areas that were burned as well as cut. The following examples of carefully aged colonies will give some idea of the growth rate of colonies of *P. ferruginea*. (1) In May 1963, a cornfield that had lain fallow for one year was burned. On 26 Jan. 1964, the 14 tallest shoots in a one acre section of this field had a mean height of 90 cm (s.d.=32 cm). The mean number of workers per shoot was 146 (s.d.=117). However, 12 of the 14 shoots had more than one young colony with workers in it. These 12 shoots had 101 founding queens and over one-half of the queens had workers in their thorns. This pasture was heavily grazed until Sept. 1963. (2) In Dec. 1962, a brushy pasture along the south margin of plot C was cleared and burned. In Oct. 1963 the ten tallest shoots in a one acre section in the center of this pasture had a mean height of 111 cm (s.d.=14 cm). Each shoot contained a single large colony and 0-6 founding queens. None of the founding queens had anything other than eggs in their thorns. The mean number of workers in the ten maturing colonies was 306 (s.d.=1.27). This pasture was lightly grazed during the entire period of colony growth. (3) In Jan. 1962, a brushy pasture along the south side of plots L and M was cleared and burned. In March 1964, nine shoots were chosen so as to be so far from other shoots that they would lack auxiliary units. They had a mean height of 294 cm (s.d.=37 cm) and each shoot contained a single colony with no founding queens. Each colony queen was fully physogastric. The mean number of workers per colony was 1149 (s.d.=297).

Workers are not found outside the thorns unless they are collecting Beltian bodies or nectar, until the colony has 50-100 workers and patrolling begins. Until control is gained over most of the thorns, so that the brood can be distributed and need not be packed in the thorns, the number of workers per thorn with brood remains high (20-40). By the time the colony is 1-2 years old, the number of workers per brood thorn has dropped to 4-20. Thorns without brood but within the patrolling range of the workers contain 0-5 workers. Even under extreme disturbance conditions it is difficult to induce more than 50 percent of the worker force to leave the thorns.

When undisturbed, workers are distributed somewhat evenly over the external shoot surface with the highest densities on the growing shoot tips and in the area of brood concentration. This density is known to rise and fall with the weather, time of day, time of year, disturbance, colony size, colony age, colony activity, the individual colony, and unknown factors. Less than five percent of the worker force is off of the shoot and on the ground or surrounding vegetation.

Some of the aspects of normal changes in the density of workers outside of the thorns of undisturbed shoots are demonstrated by the following study. Beginning on 1 Apr. and on 8 June, the numbers of workers active on the surface of the same 17 shoots along the margin of plot N-2 were counted at hourly or somewhat greater intervals over a 24 hour period (Fig. 32 and 33). The mean height of the shoots on 1 Apr. was 158 cm (s.d.=68 cm) and on 8 Jun. was 240 cm (s.d.=61 cm). Of the 17 shoots, 9 were queen-shoots and 8 were auxiliary-shoots. From both recordings, it can be seen that 1) there is a sudden rise in activity around the time of sunrise and sunset, 2) the absolute numbers of workers on the shoot is not a function of the temperature at the moment of counting, and 3) the numbers of workers per shoot is much

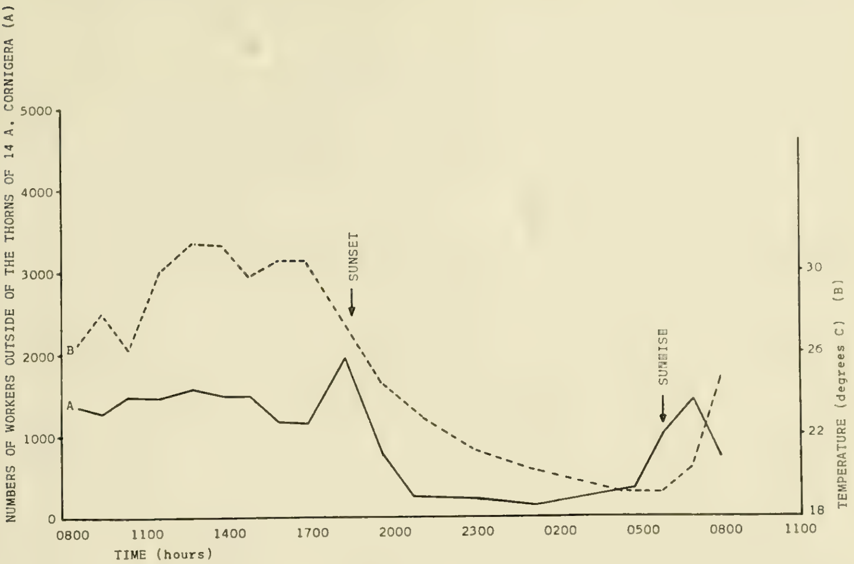


FIG. 32. Curve A represents the total number of workers of *Pseudomyrmex ferruginea* active on the surface of 14 occupied shoots of *Acacia cornigera* from 8:30 a.m., 1 April to 8:10 a.m. 2 April 1964 (dry season). The mean height of the shoots was 158 cm. A rather sudden increase in activity near sunrise and sunset, and distincitly lower activity at night, are evident from the curve. Curve B represents the air temperature 1 m above the ground throughout the period of observation.

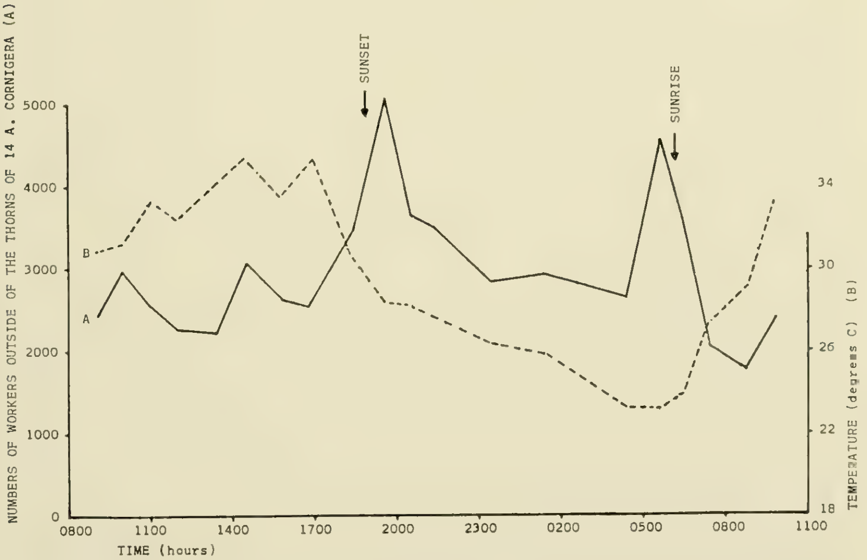


FIG. 33. Curve A is as Curve A in Figure 32 except that the counts were made on 8 June to 9 June 1964 (rainy season). The same shoots were examined. On this date their mean height was 240 cm. The same peaks at sunrise and sunset are evident but nocturnal activity was not lowered as it was during the dry season. Curve B is the air temperature.

higher during the rainy season than during the dry season. During the dry season, the early morning peak in activity is correlated with a peak in the flow of nectar from foliar nectaries. During the rainy season it is not clearly associated with any aspect of the bionomics of the tree. The reason for the increase in numbers at sunset is not clear on a direct cause-and-effect basis. Indirectly, it may be associated with the fact that just after sunset a large number of phytophagous insects become active. While in general the numbers of workers active on the surface is influenced by the temperature, within the range of 18-43° C. there are factors both internal and external to the colony which can cause substantial increases and decreases in the number of workers active outside of the thorn. Below about 18° C. the workers have trouble walking without falling off the shoot. Above 43° C. they seek the coolest part of the shoot and do not behave normally. The total number of workers in each shoot probably did not increase more than ten percent between 1 Apr. and 8 Jun. 1964. However, on 8 Jun., there were 7-27 undamaged tips on each shoot whereas on 1 Apr. there were 0-3.

Irrespective of other influences, it has been noted throughout this study that the highest numbers of workers are present on the surface of the shoot at the time when the shoot has the largest numbers of undamaged shoot tips. While many of these workers are in the vicinity of the undamaged shoot tips, the number of workers on other surfaces of the shoot also increases. This system appears to be self perpetuating because the more workers on the outside of the shoot, the higher the probability that a given shoot tip will remain undamaged.

Distribution of the alates. The first alates appear in the colony 15-24 months after the first workers. The colony contains 1000-1500 workers at this time but old senescent colonies with as few as 200-500 workers often have alates. Since alates leave the shoot daily, they do not build up to large concentrations except when cold weather prevents mating flights. A colony may contain all males, all females, or both. They do not segregate themselves nor are they segregated by the workers. Their exit from the colony does not appear to be influenced by the workers. During the cool season and the dry season, the numbers of new founding queens are lowered (i.e., fewer queens in the mating flights) and brood is absent from many shoots that contained only part of a colony (auxiliary units, which produce the majority of alates, are reduced in number and size). Following a month of cold weather which prevented mating flights, a colony with 12,269 workers had 3,421 alate females and 1,311 males on 20 Jan. 1964. Assuming an accumulation in the colony for the 30 days, this indicates a daily production rate of 0.0093 females and 0.0035 males per worker. This is probably an underestimate since there may have been an occasional morning that was warm enough for alates to leave.

Colonies occupying more than one shoot. When a colony in one shoot expands to occupy a neighboring shoot, it establishes a unit of brood and workers (auxiliary-unit) with much the same behavior and morphology of a colony in a single shoot (queen-unit) that lost its queen 1-10 weeks before. Instead of gradually dying as does a colony without its queen, the auxiliary-unit is maintained for the life of the colony except under certain weather conditions when the shoot looses nearly all of its leaves for two weeks or more. A connection is not maintained continuously between the queen-shoot and auxiliary-shoot.

The fluctuations from a status very similar to that of a queen-unit to that of an almost dead queenless unit depend on frequency of re-establishment of the trails between the queen-shoot and the auxiliary-shoot. This frequency is a function of 1) the amount of food being produced by the queen-shoot and auxiliary-shoots, 2) the size of the queen-unit, and 3) the distance between the two shoots. The number of auxiliary-units maintained by a queen-unit is likewise a function of these three variables. When the branches of two shoots are in contact, the two are occupied by the same colony if it is large enough to occupy them. If one of the two shoots contains the queen, the difference in colony structure between the two shoots is a function of colony size; if a very large colony, it treats the two shoots as if they were just two large branches from the same stump.

The maximum number of auxiliary-shoots is maintained during the rainy season. For example, on Jul. 31, 1964, the 108 emergent and occupied shoots in plot N-2 were occupied by 14 colonies. In the subplot, the number of auxiliary-shoots used by each colony was 27, 14, 14, 10, 9, 5, 5, 4, 2, 2, 2, 1, 1, and 1. This record does not include auxiliary-shoots outside of the subplot. The auxiliary-shoots of the colony with 27 were all in branch to branch contact. This colony was highly dispersed, and worker numbers were low on each shoot. The colony with 10 auxiliary-shoots was the largest in the subplot (queen-shoot had at least 10,000 workers) but its auxiliary-shoots were 1-6 m from the queen-shoot. In this case, worker numbers were very high on each auxiliary-shoot. During the dry season, the 14 colonies only had 63 auxiliary-shoots in contrast to the 98 during the rainy season.

Presence of a queen. A colony does not have more than one queen; the auxiliary shoots do not have queens. Founding queens are more commonly found in auxiliary-shoots than in queen-shoots. When present in a queen-shoot, they are in the thorns most marginal to the shoot canopy. In the auxiliary-shoot, they are occasionally found in thorns more centrally located. Founding-queens on occupied shoots are removed when found by the workers of the established colony. As a result, the number of founding-queens present inversely reflects the size of the worker force in relation to the area of the shoot that has to be patrolled. It is one of these founding-queens that establishes a new colony should the auxiliary-shoot be abandoned during the dry season by the established colony.

Abandonment of auxiliary-shoots occurs during the dry or cool season when the production of Beltian bodies falls very low. It also occurs when the queen-unit is destroyed. Abandoned auxiliary-shoots may be completely empty and in this case they should perhaps be termed "vacated" since the entire worker force and brood has moved to another shoot. More commonly, the trail between the queen-shoot and auxiliary-shoot is not re-established. This leads to gradual die-out of the auxiliary-unit (2-10 weeks); in this case, the auxiliary-shoot usually contains a few thorns with moldy brood and an occasional worker. The brood consists of alate pupae, and may be scattered through the thorns. If an abandoned auxiliary-shoot is invaded by another colony, workers coming from the original colony at a later time are killed by the workers of the new resident auxiliary-unit. In the laboratory, a group of several hundred workers and brood from a large colony, were isolated without their queen for several weeks. They killed 14 different founding-queens offered to them, but accepted a fully physogastric queen from another colony.

Placement of the brood. The fraction of the total inside volume of the thorns on the shoot used for brood in auxiliary-shoots is a function of the same three factors that influence the numbers of auxiliary-shoots maintained by the colony. In general, there is less brood in each auxiliary-unit than in the queen-unit, but the total in all of the auxiliary-units of a single colony may be larger than that in the queen-unit. The area of the shoot canopy that contains brood-thorns is usually interjected with empty but apparently acceptable thorns. There are higher numbers of alate larvae and pupae, and a lower number of first instar larvae in the brood-thorns of auxiliary-shoots than in queen-shoots. There is less volume of larvae per unit volume of thorn used for brood than in queen-shoots. Auxiliary-units show the same reactions to stress by shading and cutting of the shoot as do queen-units. Shaded auxiliary-units may subsist on products from an isolated queen-shoot or auxiliary-shoot.

Distribution of the worker force. The number of workers in an auxiliary-unit is often much lower than that in its queen-unit, but the sum of the workers in all auxiliary-units maintained by the colony may equal or surpass that of the queen-unit. On 29 Jul. 1964, in subplot N-2, a colony with 9 auxiliary-shoots (heights: 332, 226, 220, 180, 138, 126, 90, and 85 cm) and a 300 cm tall queen-shoot had 19,452 workers. The queen-unit contained 7,640 of these workers, and the auxiliary-units contained, by order of shoot height, tallest to shortest, 3,210, 2,000, 1,576, 2,624, 1,262, 207, 412, and 321 workers, respectively. Alates were present in all shoots. The four tallest auxiliary-shoots and the queen-shoot had branches in contact at the time (29 Jul.), but during the previous dry season, all of the shoots occupied by this colony were connected only by trails at ground level. It is impossible to determine the age of this colony because even though the subplot was burned in 1961, the colony was on the margin of the burn and moved into the plot following a more recent cutting of the neighboring pasture.

The number of workers in an auxiliary-unit is a function of the same three variables that determine how closely it matches the queen-unit in morphology. Since the connection between the queen-unit and auxiliary-unit is not continuous, or rhythmic, either within the day or for longer periods, the number of workers in the auxiliary-unit is likely to fluctuate much more than in the queen-unit. The highest numbers are found in auxiliary-shoots that have direct branch connections with the queen-shoot. The number of workers per auxiliary-shoot brood-thorn does not vary from that of a queen-shoot, as long as the trail between the shoots is re-established often enough to keep the auxiliary-shoot worker force from being severely depleted by mortality agents. Associated with the reduced quantity of workers in the auxiliary-unit, the number of workers active outside of the thorns is often lower than that of the queen-shoot under similar environmental circumstances; the workers are distributed on the surface of the auxiliary-shoot in the same patterns as on the queen-shoot.

Distribution of other animals in and on shoots. In queen-shoots and auxiliary-shoots, thorns tenanted by animals besides *P. ferruginea* are usually found in the same positions as are those occupied by founding-queens, i.e., in thorns in areas infrequently patrolled. *Prolepismina* sp. (La Granja, Cotaxtla), the thrips *Diceratothrips horribilis* Priesner (Cotaxtla), and salticid spiders (all sites) are commonly found in dry empty thorns with entrance holes. A small black bee (*Hylaeus* sp.) nests in empty dry thorns on unoccupied shoots in the Temascal area. Microlepidoptera larvae are occasionally found in the green or green-yellow thorns of queen-shoots. These larvae are usually destroyed before maturity. In auxiliary-shoots they more frequently complete development. The unoccupied shoots contain most such larvae.

Colonies of other species of ants are not found in queen-shoots having enough workers to patrol the shoot. However, auxiliary-units of *P. gracilis mexicana* (1-5 thorns) occasionally are found in the same shoot with a young colony or weak auxiliary-unit of *P. ferruginea*. As the *P. ferruginea* unit gains in worker strength, the *P. gracilis mexicana* unit is removed by the *P. ferruginea* workers. Other species of ants are removed in the same manner.

Occasional colonies of other *Pseudomyrmex, Cryptocerus, Camponotus, Solenopsis,* and more frequently *Crematogaster,* are found in shoots nearly or completely lacking a worker force of *P. ferruginea*. These other ants usually live in the dried thorns. They use the entrance holes of *P. ferruginea* but may modify their shape. *Crematogaster* commonly uses the exit holes of microlepidoptera. *P. nigrocincta* is treated by *P. ferruginea* as if it were another *P. ferruginea* colony and therefore the two species do not co-inhabit the same shoot except as founding queens and very young colonies. In respect to colony morphology, the interaction of *P. nigrocincta* with *A. cornigera* is indistinguishable from that of *P. ferruginea* in the study area. *Solenopsis geminata* tends *Dysmicoccus* sp. (*neobrevipes* complex) under earthworks at ground level or in the exposed canopy of *A. cornigera* but does not keep brood in the thorns. It also harvests Beltian bodies and nectar.

A few insects live a "persecuted" existence on the shoot; they are constantly being attacked. The zygopine weevil (Lechriopini near *Lechriops*) appears to be a mimic in color and behavior of *P. ferruginea*. It occasionally is encountered running on the surface of queen-shoots but is more common on auxiliary-shoots and shoots lacking a worker force of *P. ferruginea*. Its larvae live in the thorns and feed on resins that are produced in reaction to feeding damage to the strip of live tissue in the base of the thorn. The otitid fly (*Euxesta* sp.) and a salticid spider (*Metaphidippus maxillosus*) are mimics of *P. feuuginea* both in behavior and appearance. They are commonly found running among the ants on the surface of queen-shoots and auxiliary-shoots. The nests of polybiine vespid wasps are occasionally found on occupied shoots. The nests of *Polybia occidentalis pygmaea* (Fabricius) are placed on lateral branches and in shadier part of the shoot canopy. They are more frequently encountered on auxiliary-shoots than on queen-shoots. The vespids are attacked by workers of *P. ferruginea* if they land on the branches, but the wasps actively chase the ants away from the paper nest.

The placement of bird nests depends on the species of bird rather than the type of unit present in the shoot. The Derby Flycatcher (*Pitangus sulpheratus*) nests in the upper central branch forks as does the Barred Ant-shrike (*Thamnophilus doliatus*). The Inca Dove (*Scardafella inca*) nests on horizontal exposed branch forks.

Affects of stress on colony morphology. Acacia cornigera is a plant of heavily insolated habitats and shading effects the occupant colony of *P. ferruginea*. Heavy shading during the principal growing period (late May to Dec.) slows its growth and reduces the rate of production of Beltian bodies, nectar, and swollen-thorns. The Beltian bodies are paler yellow than those of insolated shoots and they may have less nutritional value. The nectar produced is less in volume and tastes less sweet. The thorns have a smaller volume, and type B thorns are rarely produced (Fig. 21a). Heavily shaded shoots only rarely have a queen-unit large enough to fill more than a single thorn with brood. These shoots are occasionally maintained as auxiliary-shoots by large queen-units and the larvae may be in part maintained on products from the queen-shoot.

Heavily shaded unoccupied shoots usually do not live more than 1-2 years; this reduces the amount of time available for a queen-unit to develop when compared with insolated shoots. Some mortality factor peculiar to shaded sites may be responsible for the lack of maturing colonies in shaded habitats. It is more probable that the apparent reduced quality of Beltian bodies and nectar, the definite reduced quantity of Beltian bodies and nectar, and small amount of space in the thorns is responsible for the usual lack of colonies.

During the cool and dry season, shoots over one year old often cease most new leaf production and drop most of their leaves; the consequent loss of Beltian bodies and nectar to the unit produces clear starvation symptoms. As adults emerge, new larvae are not present to fill their places in the brood thorns. In auxiliary-units this is because young larvae are not moved from the queen-unit to the auxiliary-unit since food is not present in the auxiliary-unit to feed them. In queen-units, the reduction of the number of thorns with brood is due to reduced egg production and slowed larval growth. In both cases, the number of larvae per brood-thorn and number of brood-thorns declines. If all food is absent for two to four weeks, the queen usually loses her physogastric condition and egg production stops. If starvation persists, the brood area becomes fragmented and takes on the appearance of a dying queen-unit or auxiliary-unit. Similar effects can be produced by killing the queen and most of the members of the unit with insecticide, or by removing the queen-thorn. Queen replacement is not suspected since in all 22 cases where the queen-shoot was deliberately destroyed, the associated auxiliary-units died. Supercedure is unlikely since the alates mate outside the colony, do not return to their own colony except by chance, and once they have left the colony are attacked by the workers if they return.

Reducing the number of thorns available to a large colony causes overcrowding. When the brood-thorns are destroyed by clipping the thorns, the small amount of brood salvaged by the remaining workers is packed into any thorn available (thorns missed and new green thorns). When intact thorns are not available in sufficient quantity, the brood is stored in the open thorn bases. The old intact thorns lying on the ground are not used as brood-thorns though founding queens and workers may hide in them. If care is taken not to kill the queen, fragmentation of the area of brood-thorns can be accomplished by cutting them partly open, and then leaving them hanging in the canopy. The brood is then removed by the workers and packed in with other brood in the remaining thorns.

MORPHOLOGY AND DEVELOPMENT OF THE POPULATION OF COLONIES. Due to the "auxiliary-shoot phenomenon," the number of colonies per hectare is not equal to the number of shoots with a worker force per hectare. There is a 1:1 ratio only if the shoots are far enough apart so that they develop a colony of their own before becoming occupied by the ants from a neighboring colony. In addition, a few naturally unoccupied shoots are present during the latter part of the dry season. The number of root systems is often much greater than the number of shoots occupied by a worker force in man-made disturbance sites. In any given regeneration cycle only a small part of the shoots are occupied and grow to maturity. On 12 Oct. 1964, following 285 days of regeneration without grazing after a cutting, plots N and O (850 m^2) had 163 emergent *A. cornigera* shoots occupied by *P. ferruginea* ($\bar{X}$ height=93 cm, s.d.=16 cm) and at least 392 shoots below the canopy occupied only by founding queens ($\bar{X}$ height=23 cm, s.d.=11 cm). It is very unlikely that more than 5 percent of the submergent shoots would have become emergent auxiliary-shoots or queen-shoots in this particular successional cycle. In natural disturbance sites, the shoots are often spaced so far apart that there are no auxiliary-shoots.

At high shoot density, the number of colonies is lowered by colony interaction. Maximum shoot density does not produce maximum colony density after the first year of regeneration. Direct branch contacts and trails between shoots occupied by two different colonies lead to aggressive merger of colonies since the workers will not tolerate foreign workers. The maximum distance that a colony will range to find auxiliary-shoots is not known, but if shoots are spaced 4-6 m apart (about 440 per hectare) the colonies in the different shoots usually do not interfere with each other. A colony will move as far as 15 m to a new shoot if the shoot it lives in is killed. If all the shoots in an area are occupied by colonies of sub-equal size, they could be closer together since there is evidence that equal-sized colonies can resist invasion by each other if the shoot branches do not touch.

At moderate densities, occupied vigorous shoots appear to be distributed with contagion since a queen-shoot is often associated with a cluster of rapidly growing auxiliary-shoots. As expected, the entire colony is distributed independently of other colonies in the area if the shoots are far enough apart so that the colonies do not come in contact with each other. This is not a static system. Ownership of auxiliary-shoots may change or a shoot may develop a colony of its own from a founding queen if it is abandoned. If an area with moderate to heavy densities of *A. cornigera* shoots is mapped and lines are drawn connecting the queen-shoots with their own auxiliary-units, the map of the field is covered with roughly evenly spaced stellate figures with variable numbers and lengths of arms. The arms occasionally cross each other and may not be straight. While the position of the queen-shoot for a colony (the center of the stellate figure) usually stays in the same place from year to year, the various colonies do not always occupy the same auxiliary-shoot each rainy season.

ENVIRONMENTAL REQUIREMENTS. Using Holdridge's (1964) classification, *Pseudomyrmex ferruginea* is found from Tropical Tropical Thorn Woodland to Low Subtropical Thorn Woodland to Low Subtropical Wet Forest to Tropical Tropical Moist Forest in the study area. Following Leopold (1959), *P. ferruginea* is found in Pine-Oak Forest, Mesquite-Grassland, Tropical Deciduous Forest, Tropical Evergreen Forest, Rain Forest, and Savanna. In all these habitats a swollen-thorn acacia is a common denominator.

It is extremely difficult to separate the environmental tolerances of *P. ferruginea* from those of *Acacia cornigera.* It is done with most ease in those areas where *A. cornigera* stops and *Acacia sphaerocephala* starts or continues (13.6 mi. S. Ciudad Mante, 11 mi. N.E. Ciudad Valles, 27.5 mi. S. Panuco, 22.8 mi. W. Conejos, 10 mi. S.E. Conejos). At these sites *P. ferruginea* continues into the drier habitats occupied by *A. sphaerocephala* while *A. cornigera* stops. Observations during the cool and dry season in the Temascal area give some clues as to the limiting factors in the physical environment at the margins of the range of *A. cornigera* and *P. ferruginea.* These are discussed below.

In the literature, *P. ferruginea* (as *P. belti* and *P. fulvescens*) is described as occurring at all *A. cornigera* sites in Costa Rica and northward, as well as at the localities of some other species of swollen-thorn acacia (Wheeler, 1913, 1942: Skwarra, 1934a, 1934b). From these reports, the general concensus is that it is an ant of lowland tropical disturbed plant communities. Museum records do not contradict this.

Host requirements. In its occupation of more than one species of *Acacia (chiapensis, cornigera, sphaerocephala, hindsii,* and *collinsii) P. ferruginea* demonstrates that it has a wider climatic tolerance than any one of them. These host-plant associations are based on Wheeler's (1913, 1942), Skwarra's (1934a, 1934b), and Safford's (1921) discussions, locality records from the literature and museum specimens, and this study. The present study has yielded no records of *P. ferruginea* living on or in plants other than swollen-thorn acacias. There are two such records in the literature. Skwarra (1934a) reports finding a small colony in a bromeliad. This was possibly a colony moving from a destroyed acacia or a misidentification. Emery (1890) reports that the type of *Pseudomyrmex belti fulvescens* was collected from the cauline swellings of *Cordia gerascanthus* by Beccari. This report is regarded by Wheeler (1913, 1942) as very exceptional and I am inclined to regard it as a migrant colony or an error in the placement of the host plant label, following the search of several hundred *Cordia* trees in Central America.

Moisture. At the margins of the distribution of *P. ferruginea,* where *A. cornigera* or *A. sphaerocephala* appears to disappear in response to increasing aridity (Tropic of Cancer, 20 mi. N.W. Ciudad El Maiz), it appears that the dryness does not kill the ant colony directly but rather that the plant lacks leaves for such a long period during the year that the ant colony dies from lack of foliar nectar and/or Beltian bodies. Most of the shoots found at these sites still had their leaves in March, but they were growing in exceptionally wet locations: arroyos and road banks. They were all occupied by well developed colonies of *P. ferruginea.* Six, two year old shoots were found growing on dry hillsides at 20 mi. N.W. Ciudad El Maiz; they had dropped their leaves and in all cases, there were no living remains of the ant colonies that had tenanted them. These shoots would therefore have to pass the next rainy season without the presence of a mature colony of *P. ferruginea.* These observations agree closely with those at Temascal where auxiliary-shoots that lose all their leaves are abandoned and at times, are not reinvaded in the rainy season.

An analogous situation is found between Veracruz and Anton Lazardo where due to some factor (probably salinity) there is a very reduced production of Beltian bodies by *A. sphaerocephala* which in turn prevents colonies of *P. ferruginea* from becoming established.

During periods of total leaf drop, it is more the lack of foliar nectar than Beltian bodies which kills the colony. This is shown by colonies that survive for several months in the dry season on shoots that produce no new leaves but do not lose all of their old leaves. Queen-shoots cut and hung in the dry laboratory have no live workers or brood after two months. Single workers confined in clean glass tubing rarely survive over 24 hours; if the cotton plug is soaked with water or a sugar solution, they may live 5-10 days. During the dry period, workers are willing to drink water and a variety of sweet fluids during the day. The pre-sunrise nectar flow is collected completely during the dry season.

With the entrance plugged by the worker, the thorn is a relatively moisture-tight container. It has a polished, hard, and relatively waterproof outer surface. The nectar brought in from the early morning nectar flow increases the total moisture content of the brood and workers inside the thorn. This moisture level probably decreases only slowly thereafter during the day even when hot and dry winds are blowing. It is possible that moisture conservation during the dry season may be partly responsible for the concentrating of brood in certain thorns rather than dispersing the larvae through all the available space on the shoot. It should be much easier to maintain relative humidity levels inside the thorn above a certain point when there is a large mass of brood rather than a little. It is possible that type B thorns are preferred as brood-thorns because their thicker walls make better insulators against drying of the contents. When it rains, thorn walls do not become soaked unless the thorns are over two years old. The refusal of the ants to use these older thorns for brood is very likely associated with this. Untended brood is often killed by fungus (following abandonment of an auxiliary-shoot or insecticide treatment). It is possible that the moisture resistant thorn wall aids the workers in keeping the inside of the thorn dry during the rainy season and thus avoid problems with fungus.

Rain has a depressant effect on the activity of *P. ferruginea.* Workers walk on branches covered with water with extreme difficulty and slowness. Therefore, considerable disturbance is necessary to bring workers out of the thorn when it is raining hard. Light drizzle only reduces the numbers outside the thorns. If free water is not standing on the branches or thorns, the workers run easily on the damp surfaces. Since most entrances are on the under side of the thorn, rain does not enter. Brood and workers in clipped thorns are drowned by rain.

Temperature. Low temperatures have a depressant effect on the activity of *P. ferruginea.* At 6 mi. S.W. Tamazunchale, 8 mi. S.W. Martinez de la Torre, 28.5 mi. W. Conejos, and Valle Nacional, *P. ferruginea* and *A. cornigera* reach their range limits simultaneously. There is heavy rainfall at each of these sites, so it is likely that it is the increasing number of days with the diurnal maximum temperature below a certain level (about 24° C.), that is acting as the range limiting factor, rather than dryness. It is not likely that the colony is killed directly on the coldest days of the year at these sites; following a night when the minimum was 11° C. (Tamazunchale) and 12° C. (Temascal), no colony mortality was recorded. At these temperatures, the workers are barely able to walk and often fall off the shoot if they leave the thorn. They can sting in this condition. A colony can be chilled until the workers are immobilized, and it recovers completely.

During the Dec.-Jan. cold season at Temascal, there was essentially no growth of *A. cornigera* shoots. The consequent reduction of Beltian body production caused auxiliary-shoot abandonment and the starvation of larvae in some queen-shoots. Much failure of Beltian body harvest was noted due to worker inactivity. However, on warm days when the workers were active, there was a harvest of those Beltian bodies present. In areas where the cool season is much longer than at Temascal, severe loss of colonies could take place through starvation.

The slow physiological growth rate of *A. cornigera* at low temperatures is decreased by the increased insect damage that occurs when *P. ferruginea* is not active outside of the thorn for long periods. This damage is mostly done by nocturnal insects. Adult katydids (Tetigoniidae) and the larvae of the noctuid moth *Coxina hadenoides* do the most damage during the cool season. It is the shoot tips that are removed by these insects, and in doing so, they are not only removing Beltian bodies, but they are also slowing their production.

During cool weather, alates hatch but do not leave the shoot, which results in an increase in the number of alates in the colony. The failure of mating flights to occur during the long cool season at the western margins of the distribution of *P. ferruginea* may be in part associated with its disappearance at these sites. During the cool season, the growth of the colony is definitely slowed. Trails between shoots are not established during periods of cool weather, and this is associated with abandonment of auxiliary-units. In addition, the slowness with which the colonies of *P. ferruginea* develop in extreme shade may be associated with the fact that diurnal temperature maxima average at least 7° C. cooler in deep shade than in full sunlight.

The most noticeable effect of cool weather on *P. ferruginea* is the reluctance of the workers to leave the thorns, and the reduced running and walking rates when they do leave. However, the activity of the ant outside of the thorn is not always directly related to temperature. This is shown by the fact that the sunrise activity peak is often at a temperature roughly equal to that of the night-time activity low (Fig. 32, 33). The sunrise activity peak is at a temperature much lower than the noon-time temperature at which lower numbers of workers are usually on the shoot. It takes a temperature of 5-7° C. higher at noon to bring equal numbers of ants onto the shoot surface than at 9:00 a.m. At high air temperatures (45-48° C.), workers and alates are driven from the thorn to lie in the shaded parts of the shoot. It is not known what the mortality is under these temperatures.

Sunlight. In general, *P. ferruginea* is an ant of heavily insolated low vegetation. Founding queens may avoid deeply shaded areas in their search for young shoots to colonize. Direct insolation can raise the temperature inside of the thorn 1-3° C. higher than the outside air temperature; this could affect larval growth rates. Light affects worker activity in that the number of workers outside of the thorns is different at the same temperature, depending on whether it is daytime or nightime. This is the case both during the dry and the rainy season. There may be almost no workers active on the shoot surface at noon when the air temperature is 22° C.; there are often many workers outside of the thorns at this temperature at midnight.

Wind. Even under disturbance conditions, the workers do not leave the thorn entrance when the wind is blowing over 25-30 mph. At this speed, they are usually blown from the shoot. Workers active outside of the thorns show no reaction to gentle shaking of the shoot by wind, but they quickly show a disturbance reaction if the shoot is further shaken by an animal.

BEHAVIOR OF INDIVIDUALS. *Larva and pupa.* The larvae are relatively inactive, even when feeding. If touched by a passing worker or with a probe, a larva begins to rotate the head in and out of the trophothylax (pouch formed by protrusion of the ventral side of the first abdominal segment; Wheeler and Bailey, 1920) while opening and closing its mandibles. Fragments of Beltian bodies are pushed deep into the trophothylax by the worker. If left protruding, the fragment is pulled in by the larva. The head is tipped completely into the trophothylax while feeding. When large food pieces that distend the pouch are eaten, the head is more externally directed so that mandibular action is visible. A roughly spherical piece of food as wide as the larva can be accommodated. If the food protrudes from the trophothylax, a worker may remove a piece or take the entire piece away, cut it up, and redistribute it. A worker may force open the trophothylax and deposit regurgitated drops of fluid there. Presumably this is honey in the laboratory and would be petiolar nectar on the acacia. While feeding, the larva ejects a clear fluid into the trophothylax with the food bolus. Yellow fragments of Beltian bodies are easily visible passing through the esophagous. These pieces are about 0.1 mm in diameter in a larva 1 mm wide.

The larvae can be fed ripe Beltian bodies by hand. They accept fragments of Beltian bodies forced into the trophothylax with fine forceps; about ⅛ to ¼ of a Beltian body from the end of a pinnule is most frequently accepted. This size fragment is that which is fed to the larvae by the workers. Beltian bodies at the age chosen by the worker for harvest are almost always accepted by the larvae when fed by hand. Less ripe ones are variably rejected when offered. If the unripe piece is placed with the rind against the mandible, it is rejected immediately or within a couple of hours. If the softer inner parenchyma is turned towards the mandibles, it is usually accepted.

Very rarely, workers are observed to capture small moths, lepidoptera larvae, and brood of *P. gracilis mexicana*. These are taken into brood thorns and presumably fed to the larvae. Wheeler and Bailey (1920) report insect fragments in the buccal pellets of *P. ferruginea*. Buccal pellets also contain pollen grains, fungal hyphae and spores, dust, and green plant tissue. On one occasion the workers in a starving laboratory colony gave a live small larva of *P. ferruginea* to a large larva as food. About one-half of the small larva was eaten. Larvae in the laboratory accepted pieces of muscle and fat body from the bruchid *Acanthoscelides oblongoguttatus* that were fed by hand. However, such insect food constitutes much less than 1 percent of the food eaten by a colony of *P. ferruginea*. There is no evidence that a colony deprived of Beltian bodies can subsist on other food.

Larvae can live for long periods without food. In the laboratory, larvae may live at least 49 days without food or worker care. These larvae are emaciated and shrunken but perform feeding motions and will accept food. This long survival ability is undoubtedly due to the large volume of fat body in well-fed larvae. Shrunken larvae are often observed in abandoned auxiliary-shoots and in queen-units that have been starved for a month or more. The ability of larvae to go without food is of clear value to isolated colonies that live in shoots that lose most of their leaves during the dry season.

Worker behavior. Worker activities in the thorn. The workers are relatively independent in their activities. They remove their own pupal exuvia but other workers occasionally help. Self-cleaning is often observed in the laboratory and on the surface of the shoot. The solid gleanings apparently go into the buccal pellet. Following accidental dunking in honey, the worker cleans iself but other workers may aid in licking off the honey. In laboratory colonies, workers are observed to stand relatively motionless for periods of several minutes. Callow workers hatched within the past 12 hours are especially inactive when in the presence of mature workers and larvae. It is not known how long individual workers remain within a given thorn, and how long before the callow leaves the thorn for the first time. One worker is usually on guard at the thorn entrance. Her antennae are often visible just inside the opening. Treating the colony as a unit, more time is spent in the thorns by the workers than in any other part of the shoot. It is not known how much of the worker's time is used in construction and cleaning in the thorn.

Little care is given to the eggs in laboratory colonies. When eggs are to be transferred from the thorn with the queen to a brood-thorn, they are carried one at a time between the mandibles. In the laboratory they are cleaned and occasionally rearranged but are not given the frequent attention that larvae are. On occasion, workers starved more than 15 days will break eggs with their mandibles and drink the fluid that is squeezed out.

Larvae receive much more cleaning and rearranging attention than do eggs, prepupae, or pupae. It is possible that workers receive some exudate from them. They lick the general body surface but do not concentrate at any particular site such as the "exudatoria."

In the laboratory, the founding queen's first 2-3 workers do little tending of the brood. These workers show little interest in retrieving spilled brood, whereas the founding queen will pull her spilled brood back into her domatia both in the field and in the laboratory.

Workers do not segregate the larval instars in laboratory colonies and there is no indication that they do so within the thorn. A single worker can pick up and carry a larva of any size. The larva is held out in front by the worker when carried and often lifted completely off the substrate. It is held at either end. Pupae are carried in the same manner. When a thorn is jarred, the brood is often packed by the workers into the thorn apex opposite the one with the entrance hole. If the thorn is progressively cut into from either end, the workers retreat, pulling the larvae after them into the undamaged portion. If the thorn contents are shaken out and the broken thorn placed on the pile of larvae, the workers retrieve the larvae. They then take them in through the regular entrance and break in the thorn.

Workers from inside different thorns on the same shoot, or from two different colonies, will work together to repack all of their spilled and mixed brood into one thorn. If a larva from one colony is placed on a flat surface of another colony's shoot, or in the trail between shoots, it may be ignored, picked up and carried into a thorn, picked up and thrown away, or bitten and the juices drunk. Which of these alternatives is followed depends on the duties of the worker which encounters the larva and how disturbed the colony is. When the larva is carried into a thorn, it is not bitten and stung as is a microlepidopterous larva before being taken into a thorn. Workers may fight over the larva in a tug-of-war fashion. Worker pupae of *P. ferruginea* from *Acacia sphaerocephala* near Veracruz were given to a laboratory colony of *P. ferruginea* from *A. cornigera* from Temascal. The pupae were accepted as well as the workers which emerged. When one colony invades a queen-shoot or auxiliary-shoot of another colony, it seems probable that some of the brood and callow workers are accepted by the victor colony.

Dead larvae are removed from the thorn. This is especially noticeable following parathion treatment. Many larvae are killed by contact with contaminated workers and perhaps by being fed contaminated buccal pellets. In such cases, ejected dead larvae often litter the foliage in the brood-thorn area.

The amount of brood in a thorn is apparently regulated by the workers. In general, the larger the thorn volume the larger the number and volume of brood that are placed in it. The actual numerical ratios vary with type of unit, age and history of the colony, and size of unit. When a small colony comes into possession of a large shoot and many thorns, it tends to use the largest thorns yet it maintains an area of brood-thorns with few unoccupied thorns in it. When there is a shortage of thorn space, such as when a new colony moves into a new set of young sucker shoots, all the thorns are packed with brood. The mechanism for the relatively even brood distribution within normal shoots may be rather simple. A worker would remove larvae when the *volume of larvae/volume of thorn* ratio passes some maximum related to 1) the volume, condition, and position of the thorn, 2) the condition of the larvae in the thorn, and 3) the number of workers on the shoot. It would presumably place the larvae in some other thorn where the *volume of larvae/volume of thorn* ratio is below the maximum. The triggering density must be rarely reached since larvae are only occasionally seen being carried between thorns. It is presumed that some adjustment process is used to keep below the triggering density, such as selective feeding of certain larvae. If all the eggs or first instar larvae found in some thorns were to grow equally fast, they would overfill the same thorn when they reach the third or fourth instar. Pupae are normally not moved between the thorns.

Unless larval cannibalism is an effective means of colony survival when normal food is inadequate, the availability of Beltian bodies and foliar nectar must set the lower limit to larval feeding rates. While some food comes from small soft bodied insects captured on the shoot, this comprises less than one percent of the food intake of a colony. The upper limit of larval feeding rate is probably set by larvel satiation. An excess of Beltian bodies is present on actively growing shoots having only very young colonies or small auxiliary-units in them; such shoots have many unharvested Beltian bodies on the leaves.

Normally, Beltian bodies are harvested as soon as ripe. When a trail between an auxiliary-shoot and a queen-shoot is re-established, the auxiliary-shoot may be stripped of its Beltian bodies that have appeared since the last trail was established. These are then carried to the queen-shoot. *P. ferruginea* does not incorporate Beltian bodies into the buccal pellet. In the laboratory a worker gives its buccal pellet or Beltian body fragment to a larva making bobbing motions with its head. Workers sometimes force open the trophothylax to remove a food fragment and give it to another larva.

Nearly all direct unaggressive interaction between workers involves food exchange. In the laboratory, the founding queen's first two or three workers show little interest in each other but as they become older, worker to worker interaction becomes involved. In older colonies, the most common worker interaction observed is liquid food exchange. Workers frequently rush head-on into each other and there appears to be antennal interplay. When one of the pair has been drinking honey, it often spreads its mandibles and a drop of fluid appears between them. The other worker drinks from this. Often the pair arrange themselves on the walls of the glass tube so that one member is upside-down to the other. This brings the hypopharngeal areas in contact without elevating the thorax. A third worker may also drink from the regurgitated drop. In the laboratory, buccal pellet interchange has not been observed. The worker that has brought a Beltian body into the tube drops it and it is picked up by another worker. Another worker also may take it directly from the bearer. Beltian bodies are carried through the thorn entrance, not passed to a worker inside. When a larva is being carried into a thorn through a break in the thorn side, it may be taken from the entering worker by one inside. Workers do not commonly clean each other except when covered with sweet substances.

The number of workers per thorn is somewhat consistent with respect to thorn volume and amount of brood in it. The thorn with the queen in it often contains over 50 workers. Brood thorns have 4-20 workers, and thorns without brood have zero to four or five. Since the thorn with the queen is not proportionately that much larger, the smaller number of workers found in brood-thorns may be related to the number necessary for brood maintenance rather than maximum tolerance of workers for each other.

Workers in the thorns are probably just as aggressive to foreign organisms as they are outside. In the laboratory, many workers in the glass tube do not hesitate to attack foreign workers or founding queens. The worker guarding the thorn entrance must recognize in some way and accept the passage of all the workers in the thorn; she backs out of the way of an entering worker.

There are distinctly more workers in the thorn with the queen than in other brood thorns. This may be due to her presence or that of the eggs'. Yet in the laboratory, the physogastric queen receives little extra attention. Her gaster is occasionally licked and workers may try to remove partly extruded eggs, though she may resist by turning and biting at the worker or walking away from her. In the laboratory, the queen is fed by the workers. Though physogastric, she is quite capable of walking without worker assistance on thorn, paper, or brood substrates. In glass tubes she has more difficulty but is still not assisted by the workers.

In moving to a new thorn, the queen is aided by the workers; they pull on her legs to help her through the thorn entrance. The workers choose the thorn with the highest volume that it located between the thorn occupied by the queen and the upper green thorns. They enlarge the entrance of this thorn in the same manner as they do that of the thorn she is leaving. She is accompanied, but not chased, by a group of workers to the new thorn. In some cases she is moved into a green thorn, but one that is hard and drying. She may move as far as 100 cm on a tall shoot.

In the laboratory, a young colony of workers without its queen will accept an old physogastric queen with only slight aggression towards her; she may be bitten briefly or stung momentarily. They will not accept founding queens. Thus a colony that has lost its queen in nature normally dies since a physogastric queen would not be available to it. A physogastric queen is not accepted by a laboratory colony that has a queen. Founding queens are always killed by foreign workers in the laboratory, in thorns, and on the shoot.

In the laboratory, newly hatched males and alate females are tolerated until they leave or die. The males often require worker assistance in removal of the pupal exuvie clinging to the genitalia. Alate females require no assistance in molting. In the laboratory, alate females have been observed receiving regurgitated liquid from workers.

The thorns are cleaned out by the workers. Unopened thorns develop a natural lacuna equal to ⅓-¾ the volume of that finally excavated by the workers. They start cutting the entrance while the thorn is still full of moist parenchyma. At this time, the thorn is green but stiff and fully expanded. They remove most of the soft tissue before it has dried and shrunk. More than one worker works on the entrance during its period of construction. One worker works at a time, until the workers are well into the thorn cavity. Two different entrance holes, one below each thorn apex, are only very rarely encountered. When this occurs, they are made by two different founding queens.

The entrance hole is nearly always in the same general position on each thorn. It is on the ventral side 3-20 mm proximal from the thorn apex. At this site the thorn is 2-5 mm wide. This is as close to the thorn apex as the worker can excavate and make an entrance that is 1.5-3 mm long by 1-3 mm wide. There is no preformed entrance or thin area in the thorn wall. The long axis of the hole is parallel to the thorn axis and the hole passes directly through the thorn wall. Dry thorns without an entrance are occasionally entered by enlarging an exit hole of a microlepidopteran, or a zygopine weevil. This entrance may be low on the thorn wall or at its base. Completely dry thorn walls are not penetrated by *P. ferruginea.* Entrance holes are occasionally started below the pointed apex of green legumes. They are not finished.

The solid material is removed in the form of pieces of 0.2-1 mm in diameter. This tissue is removed by cutting and pulling at partly freed pieces. It is seen sticking to dew-covered leaves in the early morning under the thorns in which construction is going on. These pieces have been carried to the entrance and dropped out. Smaller pieces may be incorporated in the buccal pellet. After working for periods of 2-15 minutes, a worker often goes to a brood thorn and returns several minutes later. Since the moist thorn pulp is sweet, the worker may obtain some sugars from its sap. During the cool season an unidentified bird has been observed to crush the green thorns with its beak; presumably this is done for the sweet fluid.

The entire thorn is emptied by the ants once the work has started. The thorn walls are scraped down to the hard lignified tissue that is 0.5-2 mm thick in type A and 2-4 mm thick in type B thorns. The non-entrance thorn apex is excavated to the point where the diameter of the space is 1-2 mm. The excavation of the inside of the thorn hastens the drying of the thorn walls.

Work on the entrance of a green thorn is not continuous but it is usually completed in 24 hours. Cool weather may keep workers inactive so long that some thorns are not hollowed out because the thorn wall becomes too hard to penetrate. While still visible from the outside, a worker cutting an entrance is easily distracted by disturbance of the colony. When an old entrance is being enlarged in a dry thorn to allow passage of the queen, there are as many as four or five workers ringing the hole and gnawing pieces off the lip. This work is very slow. To enlarge a hole from 1.5-2.5 mm to 2.5-4.0 mm requires 36-72 hours.

The outer margin of the thorn entrance is considerably larger than is necessary to admit a worker. Once it is cleaned of the original parenchyma, the thorn wall about 1 mm below the entrance is thickened with a hard matrix of masticated parenchyma fragments. This results in an inner entrance with a diameter closely approximating the width of the worker head (1-1.5 mm). The worker guarding the entrance remains at this point with her antennae extended almost to the margin of the outer entrance. The original parenchyma is probably too soft to be of use in this critical area. Workers that are forced to use experimentally clipped thorns may close off the entrances, which are 3-6 mm wide, with masticated parenchyma. In this case, the central entrance hole is of the same diameter as that of the inner entrance of an undamaged thorn.

Foreign and miscellaneous waste objects are removed from the thorn. In laboratory colonies, prepupal meconia, cast exuviae, dirt, and dead larvae and workers are dropped from the tube entrances. Some of this detritus may be incorporated into the buccal pellet. Grains of sand put into the thorn entrance are ejected. Shoots on sand dunes with the thorn entrances open to the wind occasionally have thorns packed full of sand, and entombed larvae and workers; the blowing sand entered faster than the ants could remove it. Thermistor probes are attacked in any thorn with workers in it. The fiberglass or fingernail polish coating of the probes is chewed off if they are left in place for several hours. Workers chew through tape placed over entrance holes, and the worker in the entrance bites introduced thread or straw.

Frass or larvae of microlepidoptera are removed from the green thorns. If a microlepidoptera larva pupates in the thorn with the consequent construction of a silk crosswall, the workers may not be able to enter the obstructed area until the moth has left. The hard and smooth silk partition is sharply angled to the thorn axis. Zygopine weevils mature in dry, unopened thorns but the workers enter the weevil's exit hole and clean out the larval frass. No external larval parasites of *P. ferruginea* have been found. Except when the brood is in a thorn with a microlepidopteran crosswall, no arthropods besides *P. ferruginea* have been found in brood-thorns.

A few insects are found in empty thorns. A single larva of a coccinellid beetle (*Brachycantha* sp.) was found in an empty thorn on a shoot occupied by *P. ferruginea.* It had an empty thorn on a shoot occupied by *P. ferruginea.* It had an abdominal convex plate which was used to plug the thorn behind it when taking refuge in the apex of the non-entrance half of the thorn. It pupated behind the plate. The silver-fish *Prolepismina* and the thrips *Dicerathothrips horridus* are found in older empty thorns in the Campo Cotaxtla area; *Prolepismina* runs rapidly and evades workers that are chasing it on the outside of the shoot. Salticid resting webs are generally found only in the empty thorns of auxiliary-shoots or shoots with no worker force. The spider can cope with an occasional worker but does not resist persistent removal attempts.

Worker activities outside the thorn. Behavior outside the thorn is separated from that inside the thorn because worker activity is somewhat different in the two areas. Activity off the shoot is an extension of that on the shoot, but outside the thorn. Activities on auxiliary-shoots differ from those on queen-shoots but these are quantitative differences rather than qualitative. These differences will be discussed under each aspect of behavior outside the thorn.

1. Routine activities on undisturbed shoots. Activity outside of the thorn is functional, either in respect to the individual worker or the colony as a whole. There are definite activity patterns and duties. These are strongly affected by disturbance and therefore are discussed separately. In general, the number of workers active on the surface of the shoot increases as disturbance of the colony increases, as the weather changes from cool to hot, as colony size increases, as shoot size increases, as colony age increases, and as the number of undamaged shoot tips on the shoot increases. A queen-shoot has larger numbers of workers on its surface than does an auxiliary-shoot of the same size even when the total number of workers on and in each shoot is the same. Not only do these factors influence the number of workers on the sur-

face, but to some extent they influence the pattern of activity on the surface. The routine activities are harvesting Beltian bodies, collecting nectar, removing damaged plant tissue, cleaning shoot surfaces, and patrolling. Less commonly observed are transport of brood and cutting of entrances into thorns.

A. Beltian body harvest. The Beltian bodies are deliberately harvested. A worker seeking a Beltian body goes directly from a brood-thorn to a shoot tip or new auxiliary tuft without making detours onto mature leaves or thorns. If pinna-end or rachis-end Beltian bodies are not available, she goes along and across the rows of pinnules tapping the Beltian bodies with her antennae and licking some. The one selected is cut and torn off at the junction with the pinnule. When engaged in removing a Beltian body, a worker is difficult to distract. They may be touched by a paintbrush and marked without showing any reaction. This "preoccupation" is accented by the fact that if the leaf is touched with the finger, patrolling workers often run to it from several centimeters away but even if the harvesting worker itself is touched, it often shows no reaction. The Beltian body is carried directly back to the thorn from which the worker came. Workers do not exchange Beltian bodies outside the thorn and they do not co-operate in their removal. A Beltian body taken from a worker with forceps and left lying on a thorn axil is usually picked up by another worker within a few minutes.

It appears that as food is needed by the larvae, a worker goes from source to source until she finds a ripe Beltian body rather than only visiting one growing point and perhaps returning without one. This behavior results in even distribution of food among the brood thorns. Beltian bodies are not commonly found in the thorns; they are not stored by the workers, but rather left on the leaves when there is an excess. In laboratory colonies, the Beltian body is cut up and fed to the larvae shortly after it is brought back. Unripe ones are ignored by the workers when placed in the glass tube.

The movements of harvesting workers are rather stereotyped. A worker returning to a thorn with a Beltian body runs with little deviation. Her speed is about 5 cm per second (32° C.). She runs to a node within one to three nodes from its thorn and starts to run out the thorn. If it is not the right thorn, she turns around before moving more than 1-2 cm along the thorn. After returning to the stem, she runs down to the next thorn. She repeats this at successive thorns until she finds her own. She avoids contacts with other workers and will even run through the middle of a frenzied group of disturbed workers without stopping.

Beltian bodies are harvested during the entire 24 hour cycle. Except when a new shoot covered with unharvested Beltian bodies is invaded by an active colony, less than five per cent of the workers active on the surface of a shoot are involved in harvesting. The rate of removal is correlated with the number of workers normally present on the surface of the shoot. When a trail is established between two shoots, there is a sudden increase in the rate of Beltian body removal from the auxiliary-shoot. These are then carried to the queen-shoot. Like other activities outside of the thorn the Beltian body harvest rate decreases as temperature decreases. During cool wather the shoot tip grows more slowly but it can be assumed that the Beltian bodies left on the leaves (due to the workers not leaving the thorns) are ripe since they are harvested when diurnal temperatures rise. The pale Beltian bodies from heavily shaded shoots are harvested in the same manner as those on insolated shoots.

The workers do not relieve the founding queen of the duty of harvesting Beltian bodies until there are 2-3 in the colony. This seems to be because by the time 2-3 workers are produced, the first worker is old enough to assume this duty. Beltian body harvest and nectar collection are the first duties to appear among new workers outside of the thorn.

B. Nectar collection. Nectar collection is much less stereotyped than is Beltian body harvest. Any worker may stop at a nectary to drink of her own needs. However, this is different from the systematic visiting which results in a distended gaster. Nectar collecting is most easily observed during the activity period at sunrise during the latter part of the dry season. The worker collecting nectar goes from nectary to nectary. When the gaster is swollen to 2-3 times its normal volume, the worker returns to a thorn and empties its crop.

During the rainy season, nectar flow is more continuous and the collection of nectar is more evenly distributed through time. At this time, workers with the gaster distended with nectar are less frequently encountered. Workers that are collecting nectar show variable responses to disturbance. Some will attack intrusive animals but are not as agile as patrolling workers. They can sting with a distended gaster.

Most of the nectar is collected by the occupants of the particular shoot, since trails between shoots are not established until 1-2 hours after the main nectar-collecting period at sunrise. Workers with distended gsaters are not seen on trails between shoots but some nectar may be carried between shoots. If the connection between two shoots is by direct branch contact, then workers with distended gasters are seen to pass from shoot to shoot.

Some other sources of liquid are available, but provide a very small part of the total liquid intake of the colony. During hot afternoons in the dry season, workers are sometimes seen collecting sap from cuts in the shoot. Some water soluble nutrients may be obtained from the parenchyma in green thorns. When Beltian bodies are cut up, juices are released which may be drunk by the workers. When small soft-bodied insects are caught and dismembered, workers cluster around the prey and drink the body fluids. Liquids from fresh bird droppings are utilized. If papaya, pineapple, or mango junces are dripped onto the shoot on hot days, workers that encounter them often drink. They do not, however, swarm to these liquids. Workers do not appear to regularly drink from drops of pure water placed on the shoot surface on hot afternoons during the dry season.

C. Workers removing damaged acacia tissue. Worker ants normally cut away damaged parts of the acacia. Despite the presence of an active worker force, phytophagous insect damage to *A. cornigera* is common. This is done by insects that are unmolested by the ants (e.g., *Syssphinx mexicana*), attacked but not removed (e.g., *Pelidnota punctulata, Coxina hadenoides*), and undetected. The stumps of shoot tips, leaf raches, and green thorns are the commonest evidence of damage. The damaged surface dries and/or darkens almost immediately. Within an hour or less a worker begins to cut away this callus or necrotic tissue. This activity is first seen in maturing colonies with 200-300 workers. These damaged surfaces may be "regarded" as foreign tissue by the worker and this excavation may be an extension of the constant cleaning of the shoot surface by the workers.

A worker removing damaged tissue acts like one cutting an entrance in a green thorn. She braces herself and partly cuts and partly tears out a chunk of tissue from 0.2-1 mm in diameter; she then turns around and drops it away from the shoot surface. A petiole stump 15 mm long may be reduced to a nub 1-2 mm high after 48 hours of this activity (with short interruptions). Only rarely is more than one worker active at the same site. If another worker comes to the site while the first is away dropping a piece of tissue, the first worker may wait until the second leaves before resuming work. Leaves and shoot tips that are wilted are pruned off. This is one of the main reasons why heavily occupied shoots usually are very clean.

The worker may obtain some materials of use from this activity. Aside from gathering sap, she may also use the fungal hyphae and partly rotted tissue of the shoot to incorporate into the buccal pellet. A worker often stops after 15-30 pieces have been removed and returns to a thorn for 1-11 minutes. She may be giving her buccal pellet to a larva.

Only a small number of workers on the surface are active in removing damaged tissue at any one time. This number depends on the amount of damaged tissue sites that are present. Shoots with a large worker force usually have lower amounts of insect damage and therefore there is less occasion for such work. Auxiliary-shoots tend to have more unremoved dead tissue than do queen-shoots. This is due to the lower number of workers per unit surface area of the shoot. Like other activities outside of the thorn, the activity of removing damaged tissue disappears at low temperatures. However, it is occasionally observed on cool nights when there are very few other workers on the surface of the shoots.

D. Cleaning shoot surfaces by workers. When the colony has not been disturbed, the majority of workers can be separated into two roughly even-sized groups on the basis of activity. One group spends most of its time running over the shoot surface and does relatively little cleaning; these are the patrolling workers which will be discussed in the next section. The other group spends most of its time licking leaf surfaces, throwing off pieces of detritus, and probing corners and crevices. These are the cleaning workers and they tend to stay in one place (e.g., on a shoot tip or mature leaf) for periods of 1-30 minutes. This results in bark, thorns and leaves being very free of foreign matter. They look as if they had been freshly washed. Cleaning workers are first evident when the colony has 100-300 workers.

The workers of very young colonies of 2-10 workers make buccal pellets long before systematic cleaning of the shoot surface begins. In view of this, it is possible that some necessary part of the larval diet comes from material obtained from the cleaning activity. In mature colonies, apparently all of the workers make buccal pellets, but the cleaning workers very likely make many more than the others. Buccal pellets from workers on shoots held in the laboratory often include sand.

The cleaning activities of *P. ferruginea* aid in normal expansion of the new leaves. All surfaces of the expanding new leaves are intensively licked. The pinnae and pinnules are forced apart as soon as is possible without breaking them. These surfaces are sticky until cleaned. On unoccupied shoots, the pinnae and pinnules are often stuck together until fully expanded. It is probable that in addition to the adherent pollen grains, fungal spores, and dust, the ants collect this sticky substance. Those workers cleaning and patrolling the growing points are the last to leave the surface of the shoot as the air temperature falls. As many as 10 workers may be found cleaning the terminal five cm of a shoot tip.

Mature leaves, thorns, and branches receive similar but less intensive attention. When cleaning a mature leaf, the worker licks exposed surfaces and probes into corners. She tends to stay on a single leaf for periods up to 30 minutes. Rarely are more than four cleaning workers observed on a single mature leaf. Usually there are less. The buccal pellets of these workers are full of dust, pollen grains, fungal spores, and unrecognizable fragments of similar size. They remove spider webs made during the night, dead pinnules, and leaf-roller webbing. Any object lying on the leaf surface is picked up and carried, or dragged, to the edge of the leaf and thrown or dropped off. Thorn and branch surfaces are treated in the same manner as mature leaves, but have a lower density of cleaning workers.

When the colony is disturbed, it becomes impossible to distinguish cleaning workers from patrolling workers because both exhibit the same attack or disturbance reaction.

E. Patrolling shoot surfaces by workers. On an undisturbed shoot's surface, a large part of the workers are patrolling and at best, only momentarily engaged in the duties described above. Many are walking or running on the branch, thorn, and leaf surfaces. They reverse direction frequently and spend little time cleaning the surface of the shoot. Most of the time, they appear to be of no direct service to the colony. These are called patrolling workers because there is a pattern to their movement, they are not distributed independently of each other, and they are responsible for most of the attacks on intrusive animals. With respect to any particular worker, she must be followed by the observer for a few seconds before a decision can be made as to whether she is patrolling or cleaning. The distinction between the two activities is largely a function of the amount of time spent running about and the amount spent cleaning the shoot surface. As the young colony grows, it is the patrolling and cleaning workers whose numbers on the shoot surface show the greatest increase. As with the cleaning workers, density is primarily a function of temperature, the time of day and the size of the colony.

The area patrolled by a worker is highly variable in size and part of the plant covered. Some representative areas are 10-30 cm of a main axis, a 40 cm lateral branch, a cluster of type B thorns, or the terminal 5-10 cm of a shoot tip. She may stay in her roughly defined area for 1-20 minutes on a warm day and for longer periods at night at lower temperatures. She stops and reverses direction frequently, and is motionless for only a few seconds. During a period of 10 minutes she might make 30 complete or partial trips through an area composed of four internodes and four type A thorns. She often runs out one or both sides of the thorns encountered. If cleaning workers are on a leaf, she often does not go out on it. If it is bare she may go out on it. When she leaves a particular patrol area, she may enter a thorn or go to another part of the shoot and patrol. If the patrolling worker encounters dirt or webbing, she acts like a cleaning worker and attempts to remove it. Patrolling workers also make buccal pellets.

The area patrolled by one worker usually overlaps that of another both in time and space. The highest density of patrolling workers on undisturbed shoots are found in the area of brood-thorns, area of growing points, and occasionally on the lower trunk.

Her perception of foreign objects appears to be primarily visual, but vibrations in the substrate are definitely of some importance. Since patrolling workers rush towards small insect-sized objects that suddenly appear in their vicinity, when these objects are 1-3 cm away, they probably are reacting to a visual stimulus. The faster an object is moving, the further away it is perceived and the quicker the worker turns toward it. In her short dashes toward objects (insects, sand particles) entering her field of perception she may run up to 15 cm per second. Patrolling workers frequently rush up to other workers but they stop suddenly at the point of contact. Patrolling and cleaning workers are usually the first to contact intrusive organisms.

If patrolling and cleaning workers are removed from some point on the shoot without disturbing the shoot, there is a definite rate of replacement of these workers by workers from other surfaces of the shoot. During the first few minutes of removing ants, the rate of replacement is high because those ants that have patrolling or cleaning duties in the area are quick to reach the point of removel. Then as the additional workers must come from farther and farther away, the rate slows to a relatively constant value. The size of this value increases as one approaches the growing points and the area of most of the brood-thorns.

The following is a representative example of worker replacement rate. On 7 Jul. 1964, four lateral branches (35 to 56 cm long) were chosen for observation on a 205 cm tall shoot containing a queen unit. Each branch had an intact shoot tip. The temperature was 34° C. (9:00-11:00 a.m.). The tip of the author's finger was held against the tip of the shoot tip and each worker that ran out on it was collected. The branch was not moved and the workers on the tip found the finger only through their normal activity pattern. This was continued for 20 minutes at each branch. The four branches yielded a mean of 20 workers (s.d.=4) per branch and was virtually free of workers with the exception of one to five cleaning workers on mature leaves. During the last 8-10 minutes of the collection, each ant removed came from the main trunk and ran out to the tip of the branch. One-half hour later, the number of workers on the branch was back to the previous level.

F. Brood and adult transport. Workers are occasionally observed carrying brood members from one thorn to another, and along trails between shoots. The larger the member, the less likely that it will be transferred. As when carrying a Beltian body, the worker runs directly, though more slowly, and is not distracted by other worker activity. It avoids other workers and may run around the branch or thorn when approached. A larva or pupa is held in the mandibles by one end. It projects forward and is held above the substrate. If the larva cannot be pushed through the entrance on the first attempt, the worker turns, backs into the entrance and pulls the larva through. At times she backs in without trying to go in forward first.

Workers are occasionally transported from thorn to thorn. The carrier holds the labial area of the one being carried and she leans back over the carrier's back. Her ventral side is against the dorsal side of the carrier. The carried worker remains inactive, with legs held against the thorax and body curved into a half-circle. The carried worker immediately becames active if the pair is picked up. The carrier always backs into the entrance with a worker. The worker being carried is usually not callow in respect to coloration. Workers have not been observed to pick up other workers outside of the thorns.

2. Trails between shoots. Passing over ground, leaves, branches, stems and vines, the trail between shoots is a bidirectional odor path. Reversal of vine or branch segments of the trail cause no confusion among workers. Even at ground level the trail tends to be confined to branches and vines. Presumably this is due to their smooth uninterrupted surfaces which act as a guide in addition to the odor of the trail. It appears that the establishment of a trail

requires that the first worker wander from one shoot to the next in such a short time that his trail stays fresh enough to be followed back. Since the distance can be crossed most rapidly along smooth and straight stems, it is probable that they will frequently become incorporated into the surface of the trail.

Workers may miss the trail. At branch or vine forks, a running worker occasionally takes the wrong fork. If such lost workers are constantly laying new trail substance, this would establish a short false trail. This is supported by the fact that the same mistakes tend to be made at the same points by different workers. Sometimes a worker does not stop when she takes a wrong turn. New trails to the shoot are thus established in this manner. Once lost she begins to wander. If she encounters the trail in this wandering, she continues along it. When lost, she usually continues in the same direction she was going previously. Workers rarely reverse direction on the trail more than a few centimeters. They run rapidly and do not stop to investigate foreign objects. On the trail, in contrast to their behavior on the shoot, they are often timid and run away from introduced objects rather than attacking them.

A trail is started by a worker wandering approximately in the direction of the other shoot. In the two cases observed, the worker started from the queen-shoot. Such a worker may be following remnants of a previous odor trail or the queen-unit may "remember" where the auxiliary-shoot is. Other workers follow and cover many segments of the path of the first worker. The new trail often follows many of the same twigs used on previous days' trails.

The trail does not always pass from the queen-shoot to an auxiliary-shoot. As many as 14 shoots may be connected by active trails at the same time. The usual number is 2-4. The trail may be as long as 12 meters between any two shoots, but is usually 0.5-2 meters in straight line distance. By going up and down vertical stems and vines, the trail maye be 2-3 times this length.

Once the trail is established, it may be retained for a few minutes up to 10-12 hours. Termination mechanisms are not understood. Presence and use of trails is correlated with colony age, colony size, distance between shoots, and the availability of food. How consistently the trails between shoots are re-established is primarily a function of these same variables. Very old colonies with few workers tend only to have auxiliary-units that are connected by direct branch to branch contacts.

A. Relation of colony size to trail. In areas of moderate to high shoot density, colonies with over 1,000 workers almost always have one or more auxiliary-shoots that must be reached over surfaces of objects that are not *A. cornigera.* The number of auxiliary-shoots increases with the size of the colony. This may be because more workers leave a large colony; therefore the chances are higher that a given unoccupied shoot will be encountered by members of a large colony. In addition, the larger a colony is, the less likely it is that its shoot will produce enough food for it. Many colonies in the

Temascal area could never maintain their size on the products of any one of the shoots that they occupy. In general, the larger the colony the longer the trails, but medium sized colonies (2,000 workers) may also have very long trails. The larger the colony the more consistently the trails are re-established between the auxiliary-shoots and the queen-shoot.

B. Distance between the shoots. The discovery of a shoot that will become an auxiliary-shoot must be done by random wandering of a worker. The further away the shoot, the lower is the probability that the worker will wander to it and return to the queen-shoot. The maximum distance over which this can be done is shortened by the fact that the longer the shoot remains without an auxiliary-unit, the greater are its chances of developing its own colony or being destroyed by biotic mortality agents.

C. Food availability and trail formation. During the cool and dry season, when growth slows in most shoots, there is increased trail forming activity in order to find shoots with Beltian bodies. This attempt is unsuccessful for the most part. During this season, worker populations are reduced in auxiliary-shoots. The total colony size decreases and many auxiliary-shoots are vacated or abandoned. When new growth occurs at the end of the dry season and during the rainy season, it is often the case that a single shoot does not produce enough food for the queen-unit or large auxiliary-unit that occupies it. New trails are then re-established. The new distribution of a queen-unit's auxiliary-unit may not be the same as in the previous season, since the same colony may not find the same shoots that it occupied previously.

D. Relation of time of day and weather to trails. Trails between shoots are established and maintained during clear or slightly overcast sky conditions. They are not consistently begun or ended at any particular air temperature. Usually, the air temperature is over 29° C. and ground temperatures may be as high as 50° C. Trails may become established, persist, or be abandoned at any time between sunrise and sunset. It appears that trail activity will persist at lower temperatures in the morning and late afternoon than during the midday hours. At night, workers have not been observed to travel between shoots that do not have contacting branches.

E. Relation of worker activity to trail formation. A sudden 3-20 fold increase in the number of workers outside of the thorns on the shoot is often associated with the establishment of a trail to another shoot. Many of these workers are not those using the trail. Between the time that the trail is established, and the time that it terminates, the numbers passing in each direcion are at best only subequal. Rates may be as high as 6 workers per minute going one way for a 30-60 minute period. Workers are often carrying Beltian bodies (usually from the auxiliary-shoot to queen-shoot) or brood (usually from the queen-shoot to auxiliary-shoot). For example, on 28 May 1964, a trail was observed between a 140 cm queen-shoot and a 46 cm auxiliary-shoot from 5:15-5:48 p.m. (31° C.). It was at ground level and 520 cm long. Three meters of this length were on a vine 1 cm in diameter. During the period of observation, 16 ants bearing Beltian bodies, and 106 ants carrying no load passed from the auxiliary-shoot to the queen-shoot. During the same period, 39 ants carrying each a larva 1-3 mm long, and 59 ants carrying no load passed from the queen-shoot to the auxiliary-shoot. One worker was carried each way. The next day, the queen-shoot contained 2,421 workers and the auxiliary-shoot contained 206.

3. Division of labor among workers. Among colonies of about the same size occupying shoots of about the same size, there is consistency in the numbers of workers on the surface of the shoot doing the same things. These numbers are highly influenced by weather and disturbance. Workers in one thorn can only communicate with those in another thorn by going to that thorn, or by chemical communication (e.g., alarm odors). Therefore, except for patrolling and cleaning workers, it is probable that the groups doing different things are relatively independent of each other. That is to say, the numbers of workers gathering Beltian bodies is independent of the number of cleaning workers (although of course the two numbers are correlated). It is only a small part of the workers in a unit that are on the surface of the shoot at any one time (less than 20 percent unless the colony is disturbed). What each individual worker is doing is apparently not related to its size but rather to its age and the amount of disturbance the colony has experienced.

A. Relation of size to division of labor. Measurements of entire colonies show only weak monomorphic allometry. Collections of workers performing various duties do not indicate that any size class is restricted to a particular duty or *vice versa*. Until a colony has produced about 2,000 workers, the mean worker size rises as the colony ages. Young colonies characteristically have smaller workers cleaning and patrolling; however, these are also the oldest workers in the colony. Workers as small as those of a colony with 50 workers, may be found performing any duty in a colony with 4,000 workers. These small workers are much more rarely encountered in a colony of such a large size because few in this size range are produced; most of those produced when colony was young have long since died.

B. Relation of age to division of labor. Since workers of all sizes may perform a given duty, it is suspected that the age of the worker dictates the duty she performs. This may explain why some small young colonies are more aggressive than some larger young colonies; the former, though smaller, have older workers. As a colony ages, the possession of a larger and larger cleaning and patrolling force may be in great part due to the increase in the number of older workers. Callow and young workers in the laboratory are less active in feeding the brood, investigating new objects, attacking introduced founding queens, and running out of the tube. Patrolling workers are almost always the darkest (and thus the oldest) on the shoot. Darkening of workers with age in laboratory colonies is related to increased aggression to foreign objects both inside and outside of the glass tube. It is probable that the successive appearance of workers that harvest Beltian bodies, collect nectar, transport brood, open green thorns, clean, and patrol in the maturing colony is associated with increase in age of certain colony numbers rather than the concomitant increase in colony numbers.

C. Relation of disturbance to division of labor. When a shoot is shaken many workers emerge from the thorns. If no further disturbance occurs, they gradually return into the thorns. The number left on the surface after the colony is calm approximates the number that were there before the disturbance. In some cases the number of workers that remain is lower. It is not known if the workers that came out of the thorns were performing a duty within the thorns. All workers will sting if handled roughly and often sting even with less provocation.

However, even with severe shaking of the shoot, it is difficult to induce more than about 50 percent of the workers to leave the thorns. On this basis, it could be said that up to 50 percent of the workers are committeed to perform the duty of defending the colony outside of the thorns while about 50 percent are committed to tending the brood. These workers in the thorns are are very aggressive towards objects entering intact or broken thorns. When an auxiliary-shoot or queen-shoot is being invaded by another colony, very large numbers of workers are outside of the thorns but it is impossible to determine which belong to which colony.

4. Reaction to intrusive objects by workers. A. Perception. Cleaning and patrolling workers are usually the first to encounter intrusive objects. Their numbers are augmented from inside the thorns to a degree related to the severity of the disturbance and the amount of alarm substance released. Intrusive objects are anything besides a swollen-thorn acacia or a member of the colony. Seedling swollen-thorn acacias are destroyed as intrusive until they are old enough to have developed the characteristics of swollen-thorn acacias. Objects are intrusive when they contact the shoot or are in the circular area around the base of the shoot where plants are attacked.

The alarm substance, a musky, rancid onion odor, is released from the mandibular glands of an excited worker. When perceived by another worker, it causes a doubling or more in running and turning rate, and produces a reaction that can be described as "rushing frantically about over the surface of leaves and branches." The worker in the thorn entrance is in an ideal site to pick up this air-borne substance and join the other workers and/or communicate with workers in the thorn. The odors released by a large colony can be carried at least 10 meters downwind to cause a disturbance reaction in other colonies. Since the colony disturbed by this odor also releases alarm substance, the colonies in a stand of shoots can become excited in a few minutes. A large disturbed colony can be smelled by the author at least 3 meters downwind. The alarm substance of one worker can be smelled by crushing the worker's head between one's fingers. Once a worker has discharged its alarm substance following rough handling, it is relatively odorless when crushed. It is not known if a worker releases the alarm substance when in individual combat with another worker, or when mauling intrusive vegetation. The odor is most evident when a shoot is shaken or a large animal moves within about 1 m of it.

The worker with its very large compound eyes can detect movement of man-sized objects at least a meter away from the shoot. A queen-unit with as few as 75 workers on the shoot surface may show a strong disturbance reaction to the movement of an observer 1 m downwind. The larger the colony, the quicker it reacts. A sheet of white paper waved nearby causes the same reaction. A group of patrolling and cleaning workers on a growing point can be excited by waving a finger 10 cm away from the workers. Workers carrying brood may be caused to run behind the branch by similar movements. No reaction is observed if the finger is not moved. If a twig or finger is waved back and forth 1 cm from a patrollling worker, she often reaches out for it. At night, small shadows produced by the light from a flashlight and that are moving on leaf or branch surfaces may be attacked. Cleaning and patrolling workers often walk past motionless insects but attack them immediately when they move. Patrolling workers frequently chase other workers passing through their patrol area; the faster the worker moves the more likely that it will be chased. While contact with the worker stops the attack, a visual stimulus appears to initiate it. The worker sees moving objects behind, in front, above, and to the sides. The reaction to movement is even more noticeable when the reaction is one of avoidance. A fleeing worker is extremely difficult to grasp with forceps due to her dodging ability.

The odor of a man or cow appears to excite a unit; slow (to avoid a visual stimulus) downwind approach often results in a disturbance reaction, though it is not as strong as when the shoot is shaken. The lepidopterous larvae *(Syssphinx mexicana, Rosema dentifera)* which are not attacked by *P. ferruginea* appear to have developed a colony odor. If one is moved to a shoot belonging to a different colony it is attacked with the same intensity as other insect species. Even the foliage on which the caterpillar is sitting may be attacked if placed on a foreign shoot.

Shaking the shoot or cutting into the trunk with a saw produces a general disturbance reaction. It is assumed that the vibration caused by chewing of *Sigmodon hispidus* has the same effect. The workers probably sense the vibration directly through the substrate. Workers seem adept at concentrating at the point of contact of the disturbing object with the shoot. Those workers accidentally contacting the area in their disturbed activity tend to stay there. While the worker runs, her antennae are sometimes held against the substrate and sometimes held in front or elevated.

B. Reaction to inanimate objects. In general, the workers remove all inanimate objects from the shoot. Dust, spores, and pollen grains are incorporated into the buccal pellet. Small dirt lumps are broken apart and the fragments dropped off the shoot. Stones too large for two or three workers to remove are eventually ignored. Spider webbing and leaf-roller webbing are pulled off though some types take several days to remove. Embioptera webs are cut through and pulled off but the workers are slow in doing it. Loose dead twigs and leaves are pulled until they fall from the shoot. Wire, string, and paint are attacked by biting and stinging. Eventually they are ignored, presumably after developing the colony odor. Banding compound ("Stikem," Michel and Pelton Co., Oakland, California) is at first attacked, but later is approached cautiously. Bird nests are usually not attacked even in queen-shoots. They eventually rot away or an occasional straw may be removed by a worker. They remain long enough for a set of nestlings to be reared. Adult and nesting birds are not attacked. In plot B, the fruits of *Muntingia calabura* were often found impaled on the thorns of *A. cornigera* after falling from the tree. The workers worked both night and day at chewing out pieces of the fruit and dropping them off the shoot. However, some workers became as distended with the sap from this fruit as they did with foliar nectar.

C. Reaction to insect-sized animals. Insect-sized animals are with few exceptions, attacked by the workers of *P. ferruginea.* These animals usually leave the shoot following the attack of a single worker. They rarely cause a general disturbance reaction. Caterpillars may require a numbers of workers to chase them before they are willing to let go of the leaf and fall. Those insects which are ignored *(Sysphinx mexicana, Rosema dentifera)* cause no change in individual worker behavior. Those which are attacked yet impervious to biting and stinging *(Pelidnota punctulata)* cause a local disturbance involving 2-100 workers and lasting as long as the insect is present. If an insect runs past a patrolling worker too fast for her to follow, she increases her speed and runs in short dashes through the area where the insect passed. If a worker encounters the leg of a large insect (i.e., walking-stick; Phasmatidae), and the insect just lifts its leg out of the worker's reach, the worker runs in tight circles and up and down the surface. If an insect shakes the leaf on which a worker is cleaning or patrolling, she begins to run rapidly over the leaf surface and may go back to the branch and out on neighboring leaves. Thirty seconds to a minute are required for her to calm down if no further disturbance occurs. Sufficient alarm substance is not released by a single excited worker for the author to smell it, but workers within 10-15 cm of the excited worker often become excited too. Some insects (especially chrysomelid beetles) often sense the presence of a walking or running worker, and jump or fall from the leaf before they are contacted.

A given worker does not invariably attack the animal encountered, but if it does, it grasps the animal with mandibles, prothoracic legs, and metathoracic legs, and stings by bringing the gaster under the thorax. An attempt is made to cling to the substrate with the mesothoracic legs. Workers pulled away from the leaf, continue to wave the mesothoracic legs in an attempt to grasp a support. If the sting cannot penetrate the object from the normal position, the gaster is moved around until a soft place is located. The animal usually leaves before the sting penetrates. At times it carries off the worker still hanging to an appendage, but often the ant releases its hold immediately after attacking. Small soft bodied insects (Lepidoptera larvae, moths, brood of *Pseudomyrmex gracilis mexicana,* aphids), are sometimes held and stung until they are paralyzed. A single sting of a few seconds duration behind the head is usually sufficient to paralyze a 1-cm-long geometrid larva in 20-30 seconds. A larva the size of a worker may be carried to a thorn and presumably used as food for the larvae. However, competition often develops between the workers that attack the larva, and often they try to hold it against the pull of the worker trying to carry it away. A third faction develops in the form of workers that attempt to take the dead larva and drop it off the shoot as if it were a bit of detritus. If the larva is larger than a worker, it takes several workers to hold it down and requires a series of stings to paralyze it. As more workers gather at the scene each tries to pull the larva in a different direction. A few workers cut into the larva. The larva is eventually stretched and torn into pieces which are then carried to a thorn (rarely) or dropped off the leaf (usually). There appears to be no co-ordination of activity on the part of the workers. Workers never cooperate in the transport of a piece of larva. Each one treats the larva as if she were the only ant attacking it.

Founding queens are often killed by the workers of the shoot on which the queen attempts to establish a colony. When founding queens are being removed from thorns, the worker grabs one of the queen's antennae with her mandibles, and pulls until the queen is partly out. Then she tries to sting the queen. If the worker is successful in removing the founding queen, they may become entangled and drop to the ground with the worker stinging the queen. The queen also tries to sting the worker. The worker kills the queen in most cases. On the shoot, the worker may drag her around by an antenna or leg until she escapes or the worker is joined by others. Several workers may attack the same founding queen.

The only obvious relation between the size of the insect and frequency of worker attack is that big insects are easier to find, usually slower, and move the foliage more. Whether or not the insect is phytophagous of habit seems to have little bearing on the attack. Movement by the insect, and particularly the jerkiness of this movement, is of great importance. The placement of the insect on the shoot influences the probability that a worker will encounter it, and the probability that the worker will be aggressive toward it. For example, an insect on the uppermost terminal shoot tip of an occupied shoot, in the rainy season, is normally attacked within a second or less. That not all insects are attacked is due to the insects' properties, the particular worker encountering the insect, and the numbers of workers active on the outside of the shoot.

Those variables which influence the number of undisturbed workers on the outside of the shoot also affect the efficiency of the unit in removal of small animals from the shoot surface. Since phytophagous insect activity decreases greatly during cool or dry weather, decrease of worker activity at these times may be less critical than it would be during the growing season. However, there is enough phytophagous insect activity during the cool and dry season so that when combined with the physiological reduction in shoot growth rates, the result is that intact shoot tips on lengthening branches are almost nonexistent during this period of relative worker inactivity. During the dry season, workers are less active on cool nights and the larvae of the noctuid *Coxina hadenoides* do heavy damage. During the growing season, many workers are active at night as well as day and they are effective in lowering the incidence of many nocturnal feeders.

The workers of *P. ferruginea* are effective in keeping other insects off the shoots both during the day and night. This is shown clearly in Table 2. This data was obtained by direct counts of the insects present on occupied and unoccupied shoots between 13 Jun. and 29 Jul. 1964. All species of ants, bees, wasps, and flying lepidoptera are excluded in the counts. The shoots were in control and experimental subplots and at each recording, all shoots in a given subplot were examined. Since some colonies do not have workers active outside of the thorns on cooler nights, these plants were recorded as unoccupied even though they contained a colony. However, these plants constitute less than one percent of the sample. Night-time recordings were made with a flashlight. No recordings were made in the rain. No subplot was recorded within five hours of the previous recording. Over 90 percent of the unoccupied shoots were in treatment subplots and over 90 percent of the occupied shoots were in control subplots.

The insects found on occupied shoots (240) have quite different characteristics from those found on unoccupied shoots (3124). Of the 240 insects, 88 were larvae of *Syssphinx mexicana*, 63 were larvae of *Coxina hadenoides*, and 40 were adults of *Pelidnota punctulata*. *S. mexicana* is not attacked unless it begins to feed on the uppermost undamaged shoot tips; all 40 of the larvae were on mature foliage. *C. hadinoides* is attacked by *P. ferruginea*, but unless the frequency of attack is high, it is not removed. *P. punctulata* is attacked persistently but ignores the workers. Most of the other insects present on occupied shoots were being chased off at the time of recording or were on shoots with only a few (5-25) workers active outside of the thorns. There were 3 *P. punctulata*, 43 *S. mexicana* and 182 *C. hadenoides* among the 3124 insects on unoccupied shoots. A sample of worker effectiveness of this type

TABLE 2. Incidence of phytophagous insects at night and during the day on shoots of *Acacia cornigera* occupied by *Pseudomyrmex ferruginea,* and on unoccupied shoots, during the first part of the 1964 rainy season.

Day	Occupied	Unoccupied
No. of shoots examined	1,241	1,109
No. of shoots with insects	33	427
No. of insects on the shoots	48	977
No. of insects known to feed on *A. cornigera*	45	894
Night		
No. of shoots examined	847	793
No. of shoots with insects	109	466
No. of insects on the shoots	192	2,147
No. of insects known to feed on *A. cornigera*	187	2,114

is complicated by the fact that once an unoccupied shoot has had its new foliage and shoot tips removed, and has ceased growth, many phytophagous insects are no longer interested in the shoot as a source of food and therefore do not remain on the shoot.

Since queen-shoots have more activity outside of the thorns than do auxiliary-shoots, the thoroughness of removal of animals is likewise greater on queen-shoots. Patrolling and cleaning activity is heaviest in the central thorn area and on new growing points. Animals are almost never seen in these areas on a shoot with a worker force outside of the thorns. Less continuous patrolling and cleaning activity is necessary to insure the removal of sedentary phytophagous insects (aphids, mealy-bugs).

D. Reaction to large animals. Shaking the shoot by a large animal appears to cause a disturbance reaction by the entire colony. In a small young colony, it may cause all the workers outside of the thorns to hide in the foliage or enter the thorns. During heavy winds or cold weather, only a few workers will leave the thorns if the shoot is shaken and these soon fall off or return to the thorns. The usual reaction to shaking the shoot is an increase in the rate of movement and in the number of workers on the shoot surface. For example, on 11 May 1964, the main axis of a 95 cm tall shoot was tapped sharply 20 times with a pencil at 9:30 a.m. (34° C.). Within 30 seconds, the number of workers outside of the thorns rose from 52 to 130. Four and one-half minutes later (no further disturbance) the number had fallen to 65 workers on the outside of the thorns. This shoot contained a queen-unit with about 500 workers in it. The number of workers outside of the thorns of a 250 cm shoot under similar conditions rises from about 250 to 350 workers, and falls to the previous value in about 10 minutes. A similar rise in activity may be associated with the recent establishment of a trail to another shoot, invasion by another colony, perception of the body odor from a large mammal, or visual perception of such an animal near the shoot. This increase in number of workers outside of the thorns should not be confused with normal increases in activity such as those at sunrise and sunset. Following severe disturbance, it may take an hour or more for the activity on the surface to return to normal levels. It is very difficult to determine normal levels since worker behavior is frequently modified by animals, wind, rain, changes in temperature, and the activity of the colony itself. The rate of return to normal levels of activity increases as the temperature decreases.

The reaction to a large animal is varied in the individual worker, but consistent in colonies with more than 200-500 workers. When foliage is torn or chewed from the shoot, it may take a few seconds to a minute or more for a general disturbance reaction to take place. The patrolling and cleaning workers on the growing points react immediately. There are those workers which do not attack (Beltian body harvesters, nectar collectors, etc.) but the colony always contains workers that will. Further, it appears that the more alarm substance released, the more workers there are that will leave the thorns. The ability to react to alarm substance apparently increases with increasing age of the worker. The attacking worker runs out onto the contacting animal and usually bits, stings, and tries to pull away after a second to a minute or more. The barbed sting sheath often holds her in place. She also releases alarm substance. It is possible that this alarm substance serves as an aposematic stimulus to browsing mammals (cattle, horses, goats, deer, cricetid rodents). It would be especially helpful in recognizing *Acacia cornigera* at night.

E. Worker damage to plant parts. When diurnal temperatures are over 26-28° C., any plant that does not have the characteristics of a swollen-thorn acacia, and contacts the shoot, may be mauled by a worker (Fig. 34, 36-38). There is a circular area under the shoot in which other plants are also mauled (Fig. 35); this produces a circle of bare ground varying in diameter and distinctness that is usually not greater than the diameter of the canopy. Shoots with over 200-500 workers that have occupied the shoot for several months or more are free of vines and do not have growing branches or shoots of other plants within the canopy. There are some exceptions to the above statements.

The plant part is mauled and this results in a blackened necrotic area. The workers persist until contact with the *A. cornigera* shoot is lost due to withering of the plant part (Fig. 37 and 38). On the ground they persist until all green or soft tissue is gone . There are often large nobs of callus tissue on the ends of intrusive branches that have repeatedly tried to produce leaves. On branches with leaves, the petiole is attacked and the leaves fall off. In open grassland, there may be no more than a patch of bare dirt around the base of the trunk (Fig. 35b). When the shoot grows in roadside mats of vines there is a small hole in the mat where the trunk comes through, and no vines use the shoot as a standard. In dense vegetation, this activity produces a cylindrical space free of foreign vegetation around the shoot. In the produc-

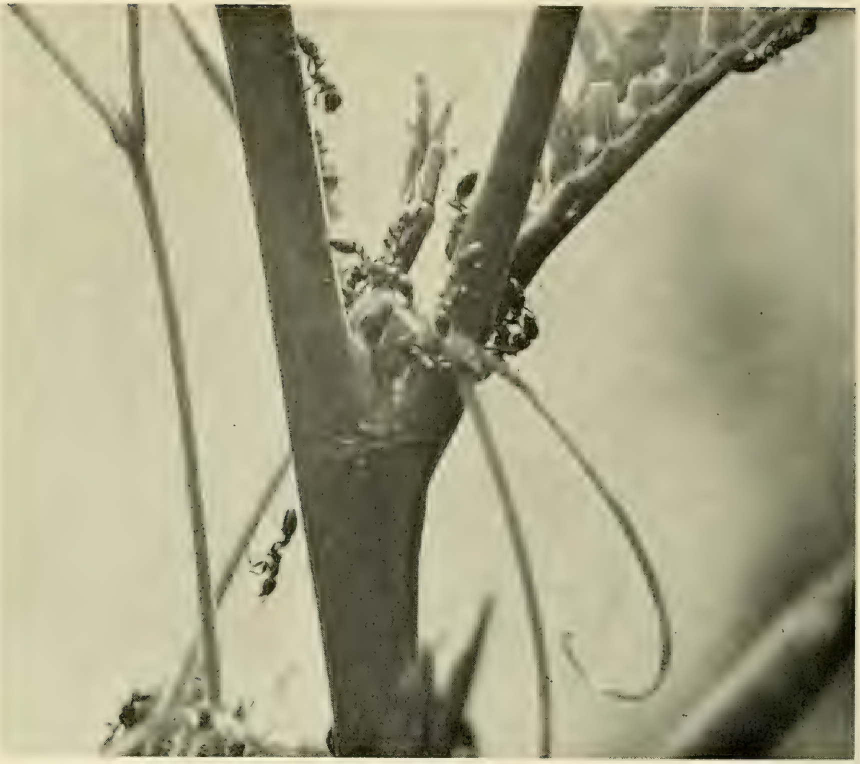


FIG. 34. Workers of *Pseudomyrmex ferruginea* attacking the tendrils of a vine of *Ipomoea* sp. that was placed over an upper node of an occupied shoot of *Acacia cornigera* a few minutes before. Within five minutes, the more slender tendrils had been pruned off. Three of the workers in the area of the thorn axil are biting into the tendril. The number of workers in the photograph is representative of those usually present around a foreign object of this size that does not move. Photo 1 Aug. 1964 in second growth vegetation 7 km east of Temascal.

tion of the cylindrical empty space around the shoot, the growing points of other plants are mauled when they contact the shoot. The workers may chew them for distances up to 30-40 cm back from the point of contact. The subsequent death or leaflessness of the branch over this distance leaves a gap between other green plant matter and the shoot. If the base of the other plants are within the basal circle, the workers travel up the stems to the growing points and destroy them if they are equal to the *A. cornigera* shoot in height or lower (Fig. 38).

If a vine or branch falls across the shoot, the workers may not be able to remove it but they often kill such a stem by girdling it. The reaction to a foreign plant may be immediate or it may take a few days of warm weather for damage to appear. A tender vine tip (Convolvulaceae) may be killed in a few minutes. The rapidity with which an intrusive plant part is removed is

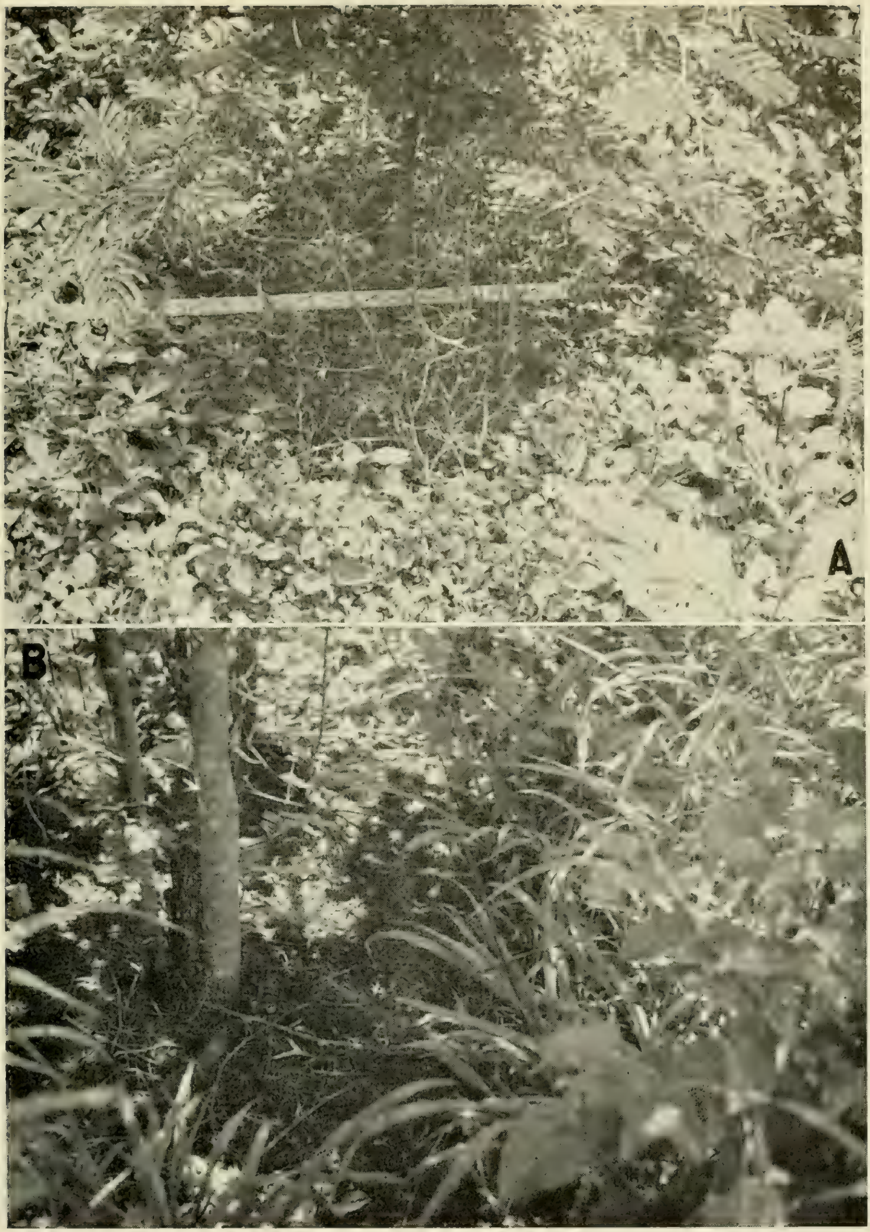


Fig. 35. a. The basal circle under a one year old queen-shoot occupied by a large colony of *Pseudomyrmex ferruginea.* The shoot was 165 cm tall. The basal circle is 40 cm in diameter and is completely devoid of living leaves of other species of plants. The leafless woody stems are those that sprouted from old root stock at the site before the colony of *P. ferruginea* had grown to a size sufficient to keep them pruned. All annual herbs and vines that sprouted in the basal circle were killed in the seedling stage from mauling by the workers. Photo 27 Jul. 1964, in second growth 7 km east of Temascal. b. The basal circle under a two year old queen-shoot occupied by a large colony of *Pseudomyrmex ferruginea.* The *Acacia cornigera* was 400 cm tall, and was a sucker from an old cut stump that can be seen between the bases of the two main suckers. The basal circle is about 100 cm in diameter. Its freedom from foreign living plants of any kind is due to the cumulative effect of two years of mauling by the ants. Further, any small seeds that fall into the basal circle are carried outside of it and dropped by the workers. The density of workers in the basal circle was about 1 per 200 cm^2. This site was burned on 19 May 1964; the basal circle was sufficiently free of dead plant matter so that the fire did not approach close enough to scorch the bark and kill the shoot. Photo 27 Jul. 1964 in regeneration after a fire 5 km east of Temascal.

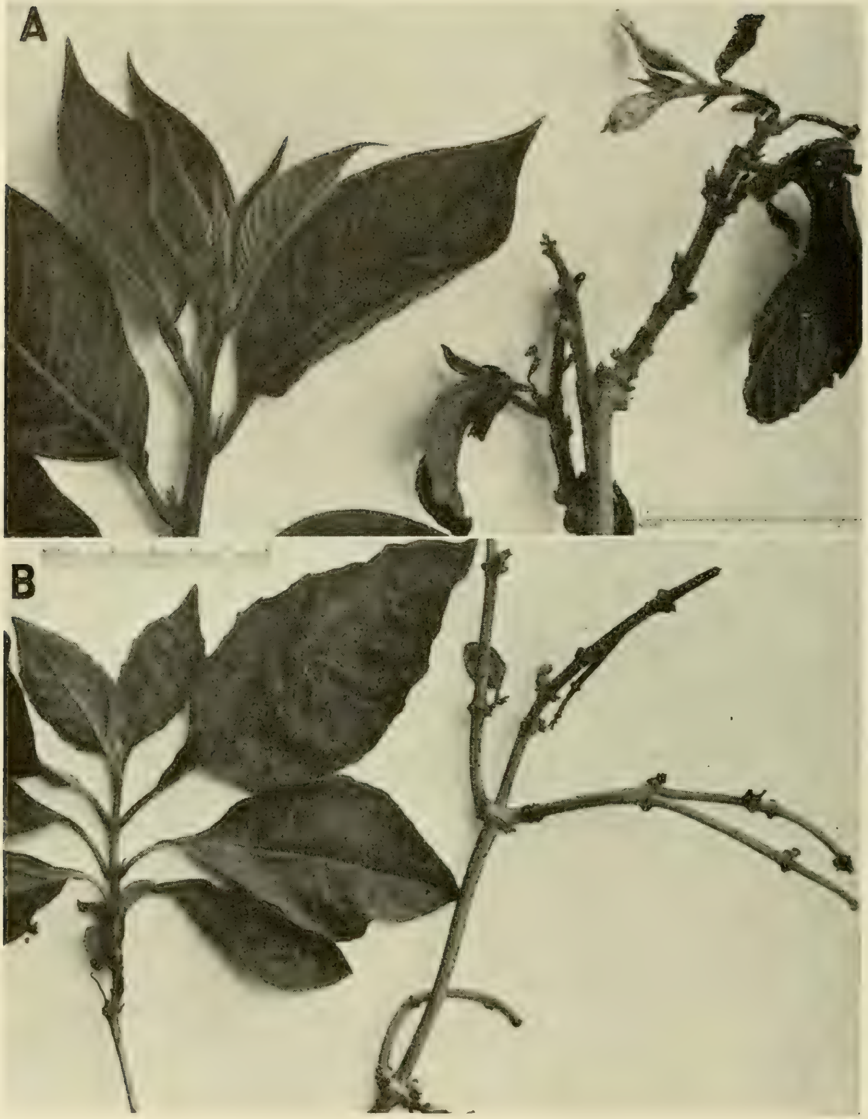


FIG. 36. a. On the left, a normal shoot tip of *Tournefortia hirsutissima.* On the right, a shoot tip of *T. hirsutissima* that began to grow into the canopy of an occupied shoot of *Acacia cornigera* and was mauled by *P. ferruginea.* Both of these shoot tips are from the same individual plant and are of subequal age. It is this type of mauling activity that keeps the occupied shoot free from vines and that produces a cylindrical space around the shoot that is relatively free from foreign vegetation. Photograph taken in late June, in plot P. b. As in Fig 36a except that the plant is a woody vine-shrub.

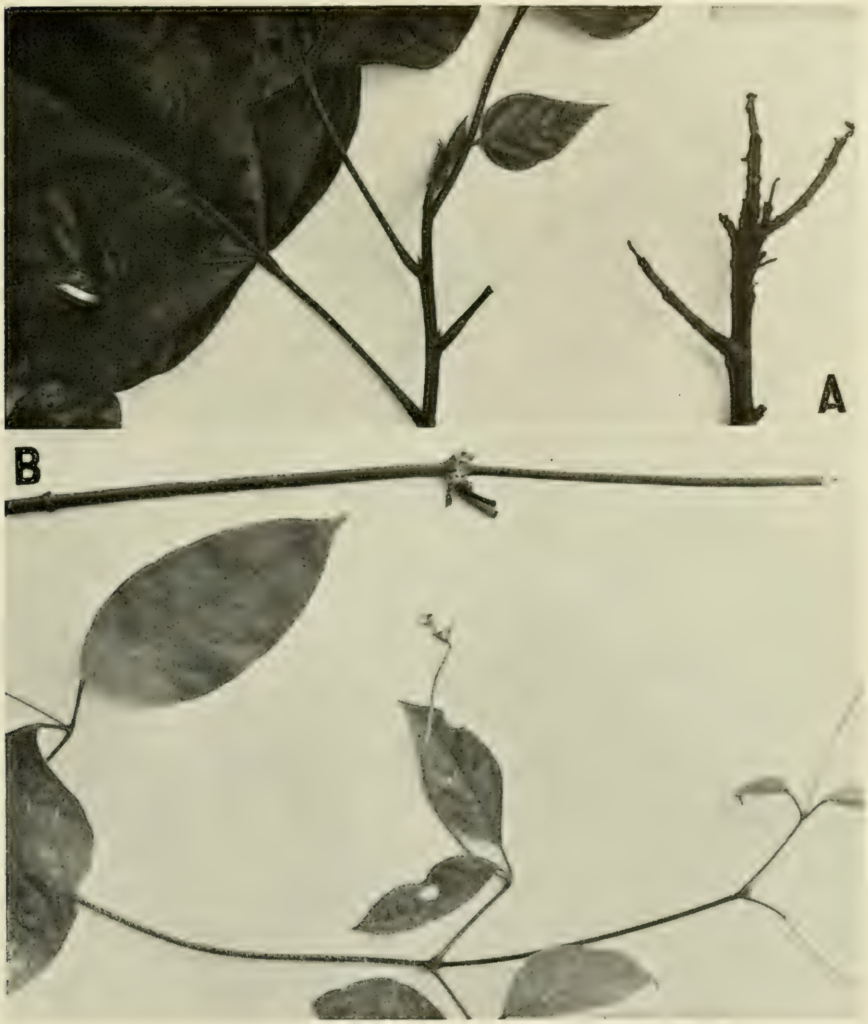


FIG. 37. a. As in Fig. 36a except that the plant is the shrub *Bixa orellana*. b. As in Fig. 36a except that the plant is the vine *Bignonia unguis-cati*. The upper shoot tip grew into an occupied shoot.

an increasing function of colony size and diurnal temperatures. The size of the lateral and basal clear area is definitely associated with the individual colony as well as its size. The workers in young colonies start mauling other plants when there are about 200 workers in the colony. Workers mauling foreign plants are easily distracted; they are often aggressive to the distractor.

Some sap or plant tissue may be collected during the mauling. It is not likely that mauling of plant parts is a simple gathering of food because it is least noticeable during the dry season when produce from the shoot is lowest in quantity, and it ceases at such a short distance from the shoot.

Workers on trails between shoots usually ignore the green plant matter that they walk on. However, the vines that are used for trails sometimes come in direct contact with the shoot and are mauled at this point. When mauling is done along a trail it is done to lateral growing points of the vine.

With the exception of some terrestrial bromeliads and Agavaceae, the growing points or leaves of all intrusive plants are successfully mauled. Cases of little or no damage to intrusive foliage are associated with unoccupied shoots, small auxiliary-units in large shoots, cool weather, or very recent growth of the intrusive vegetation. Very pubescent growing points, corky branches, and coarse-leaved grasses are most slowly damaged. Seedlings of swollen-thorn acacias without swollen thorns, Beltian bodies, and leaves with petiolar nectaries, are destroyed.

Behavior of reproductive female. Inside the thorn before copulation. In laboratory colonies, alate females that are 12-36 hours old have been observed receiving regurgitated honey from workers. They spend much time standing motionless in the tube and do not react to the presence of brood in a recognizable manner.

Outside the thorn before copulation. Alate females leave the thorn 1-3 days after emerging. Workers have not been observed to restrain alates from leaving in laboratory colonies or in the field. When a thorn containing alates is broken open, no effort is made by the workers to restrain the alates that leave. In the laboratory, they leave the brood thorns singly ½-2 hours before actual sunrise (sunrise as here used means actual appearance of the sun above the horizon). They run about on the thorn for 1-10 minutes and then fly to the screened window. On this window, males pay no attention to females.

In the field, alate females have been observed with a flashlight to leave the shoot 80-42 minutes before sunrise. They fly rapidly out and up in a straight line and in the dark it is not possible to follow this flight. Some ignore the flashlight but others fly to it. There are no records of *P. ferruginea* being collected at lights. They are seen running on branches and the main axis of the shoot, generally in an upward direction. While most fly from the top of the shoot, some leave from lower points. There are large numbers of workers on the shoot at this time but those encountering the alates ignore them. Air temperatures are usually 22-23° C. (range 21-25° C.). No exit has been observed during rain or drizzle. When diurnal maxima are in the 18-24° C. range, the alates do not leave the shoot.

After leaving the shoot, she flies upwind to a tall object in the area of the shoot; mating swarms have been observed on telephone poles, palms, rooftops, and broad leafed tree tops. All such substrates stand well above the surrounding vegetation. She lands on the substrates 5-15 meters above the ground. She stands for a few seconds and then elevates the gaster and opens

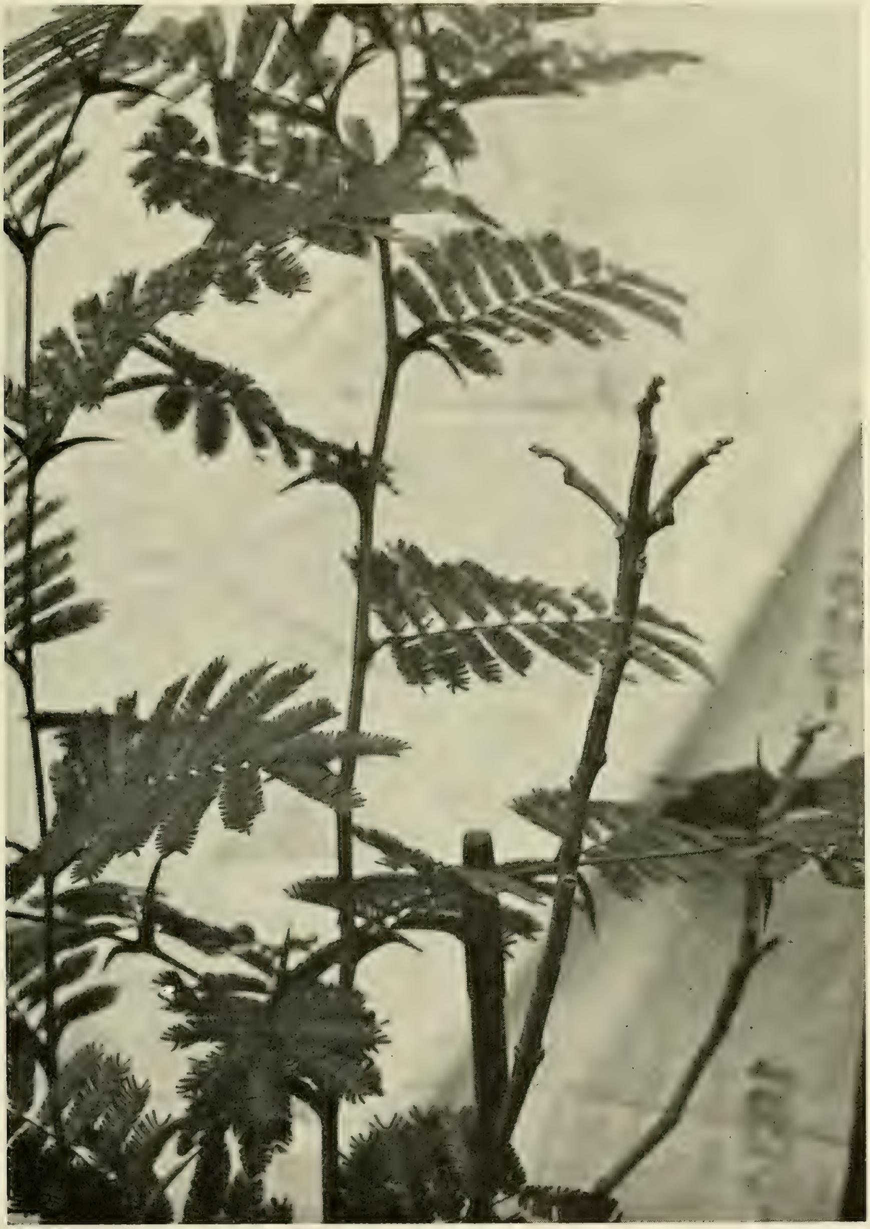


FIG. 38. On the left is a portion of the canopy of an occupied *Acacia cornigera*. On the right is a leafless shoot tip of an unidentified shrub in the Leguminosae. The base of the shrub was in the basal circle of the acacia and the acacia grew upward to encompass the shrub. The leaves of the shrub were then killed by the workers of *Pseudomyrmex ferruginea,* and any new buds were likewise killed. Photo November 1963 in plot I.

the sting chamber. The sting is fully extended and pointed upward. Presumably she is releasing a sex attractant at this time. She holds this position until one of the males running on the surface encounters her and mounts to copulate. Once the genitalia are joined and the male stops moving, copulation lasted exactly 10 seconds for five timed pairs. At the end of copulation, the female turns and begins to bite and push the male off. At this time, the pair usually falls free. They break apart while spinning earthwards or immediately after landing. During high swarming activity, as many as 500 pairs in copula may drop from the swarm in 15 minutes. On Jul. 28 1964, it was estimated that 3,000 newly impregnated queens were produced by the three mating swarms in the trees over 2 acres around plots K, P, N, and O. During the later part of the dry season, there were some mornings when not over 10 copulations took place in a single swarm. A large spider, *Selenops galapagoensis,* and the vespids (*Polybia occidentalis pygmaea,* and *Stelopolybia areata* (Say)) which prey on the males have not been seen to capture females.

Outside the thorn after copulation. Immediately upon breaking away from the male and alighting on a surface, the alate queen stands still, elevates her gaster, and pumps the terminal segments of the gaster. This action lasts 30-60 seconds. This presumably works the sperm packet into the spermatheca and closes the genital chamber. After the gaster is lowered, she stands for 1-15 minutes on the substrate and then runs or flies away. Observation of this activity is facilitated by spreading a sheet below the mating swarm. These females show negative phototaxis to strong lights. They will sting at any time.

The search for *Acacia cornigera* shoots begins immediately. If a shoot is encountered at this time, the newly impregnated queen reacts to it in the same manner as a female which has been searching for at least a day. A tracing of the route of a searching alate female has the appearance of a long string scattered on the floor. She flies short hops of 5-200 cm and runs over leaf and stem surfaces. At a distance, the shoot lacks an odor or sight attraction to these females. Frequently a searching queen flies or runs within 5-20 mm of a leaf or trunk of *A. cornigera* and does not turn toward it. Later, upon touching the same or a different shoot, she stops and investigates. She often covers the same general area or plant surface two or more times and tends to stay within 1-3 meters of some arbitrary point for 10 or more minutes. Alate queens do not search at night or when diurnal maximum air temperatures are below 24° C.

Upon touching a small unoccupied shoot, the searching queen runs onto it and then over most of the branch and trunk surfaces. She shows a definite avoidance reaction to other queens and insects by backing rapidly away and/or running around to the other side of the stem, and then either running or pausing motionless. She may jump off. If she does not wander off, and is not scared off by another queen or insect, she begins to pull off her wings with hind and mid-legs within a few minutes. This may take up to 10 minutes. When dealate, she wanders about over the surface of the shoot examining entrances. If she finds a thorn without a queen, she enters and does not leave except for food. If all are occupied, and she finds a new green thorn, she often begins to construct an entrance hole. If not distracted, she will continue until out of sight. This work is continued at night and requires 10-25 hours.

If a thorn is not available, she may wander off, stay on the shoot until eaten by a predator, or be scared off. She also may enter and occupy a thorn temporarily vacated by another founding queen searching for food. The starved brood occasionally found with a founding queen indicates that the invading queen may not adopt the strange brood. If she can gain entrance, a searching queen may fight with the resident founding queen. On two occasions a thorn has been opened when a founding queen and a searching queen were fighting inside. A dead queen is occasionally found in a thorn with a new founding queen in the entrance. On one occasion, a founding queen was observed to throw the fragments of a decomposed founding queen out of the thorn entrance. When there are two entrance holes in the thorn, one queen positions herself in each entrance. There is no evidence that either of these queens survives to rear brood in such a thorn. Two queens will not tolerate each other and one cannot guard both entrances. In the morning, in an area where there are large mating swarms, as many as 36 dealate females (searching queens) have been found on the surface of 25-45 cm tall *A. cornigera* shoots growing on bare ground (Fig. 9).

When a searching queen encounters a shoot with a worker force, she searches it the same manner as an unoccupied shoot. Normally, her contacts with workers are so frequent that she quickly drops off. If she is caught and held, she is killed by stinging. Usually the worker that catches her leg drops off with her to the ground. Since auxiliary-shoots often have a lower worker force than queen-shoots of the same size, she has more chance to find an unoccupied thorn and enter it. She cannot return to her parent colony without being killed by the workers.

Once having left the shoot for any of the above reasons, she wanders until she finds another shoot or dies. Some queens undoubtedly examine large numbers of shoots before they die. Searching queens are commonly found wandering on the ground and on low stems. They may leave shoots of *A. cornigera* and hide in hollow twigs during hot afternoons, and return to the shoot at night. In glass tubes without food and water, dealate queens may live at least 18 days. They can therefore search for this length of time, and probably longer since water and nectar are available in the field. They are most active on the shoots in the early morning and late afternoon. During the mid-day hours they are often found motionless on shaded parts of the shoot.

In the field, there are many more searching queens than there are new thorns on unoccupied shoots. On hot days in the rainy season, searching queens are as dense as three per m^2 of three months old regenerating vegetation. The number of searching queens seems greatly reduced during the cool and dry season, but founding queens are still relatively abundant in the thorns. Eventually, the maximum number of colony queens is one per shoot. Therefore, high mortality must occur among searching and founding queens. During the dry season, searching queens constitute a major part of the diet of the lizard *Sceloporus variabilis.* It is commonplace for the stomach and intestine of a single lizard to contain the remains of 5-30 queens. Bird droppings frequently contain queen head capsules. Spiders (e.g., *Dipoena ocosingo, Tmarus ineptus, Corythalia* sp.) are commonly found on and off the shoot with searching queens as prey.

Searching queens are not aggressive. They see well and are very alert to movement. They notice hand movements at distances of 20-100 cm. Queens sting when picked up and squeezed. In a tender area of skin, they can cause the same amount of pain as a worker.

When a searching queen encounters a shoot of *Acacia chiapensis*, she reacts to it in the same manner as to a shoot of *A. cornigera*, except it takes her much longer to cut the entrance hole. On those shoots that have hard thorn walls and a tough inner parenchyma, she often only clears out enough of the parenchyma to admit her body. She is not successful in rearing brood in these cases. A three meter tall shoot of *A. chiapensis* may have several hundred thorns with entrances made by founding queens of *P. ferruginea;* these thorns are almost invariably empty. An established colony of *P. ferruginea* in a shoot of *A. cornigera* is quite willing to use an adjacent shoot of *A. chiapensis* as an auxiliary-shoot (Fig. 39).

Inside the thorn after copulation. The queen that enters an empty or new green thorn takes up a position with her mandibles 2-4 mm inside the exterior margin of the thorn entrance. Her antennae can often be seen immediately inside the entrance. She is usually found at this point in thorns torn from the shoot, or cut open while still on the shoot. Thorns on small shoots that have never been tenanted by a worker sometimes have an entrance constricted with masticated parenchyma. This construction work must have been done by a founding queen. She cleans a green thorn completely, and removes the parenchyma in the same manner as the workers.

Her eggs, brood, and first workers are found scattered throughout the thorn. By the time the young colony has grown to where the thorn is packed with brood and workers, a worker replaces the queen at the entrance. In laboratory colonies, even when accompanied by her first 2-3 workers, it is the queen that faces the 4 mm diameter tube entrance and goes to investigate Beltian bodies and other objects placed on the tube lip. In laboratory colonies, the founding queen spends some time licking and rearranging the larvae.

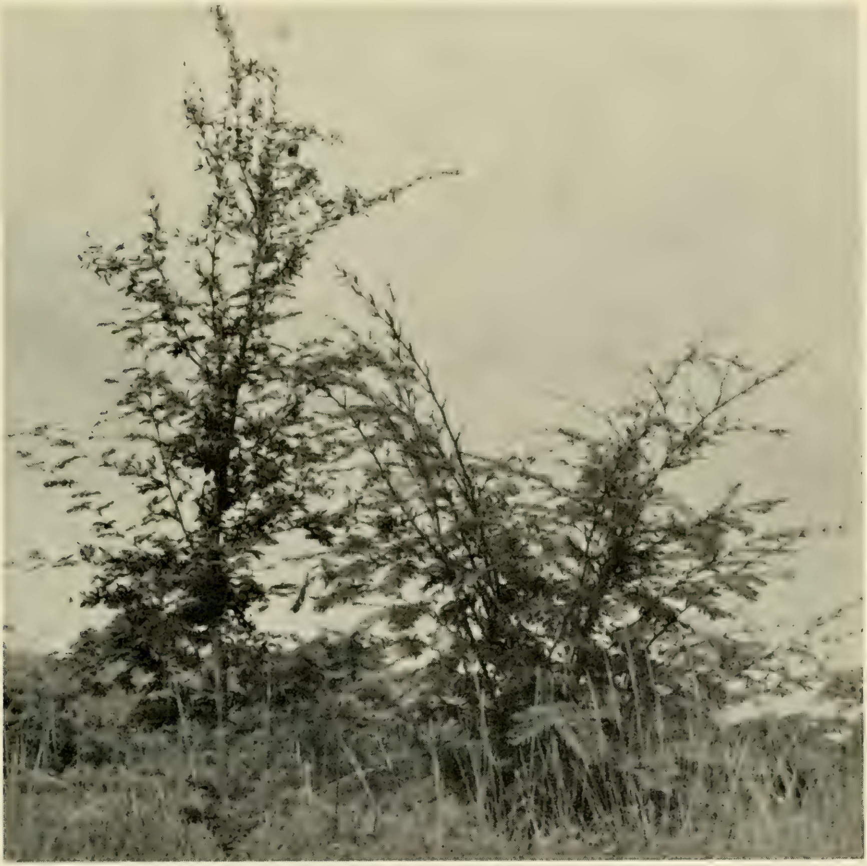


FIG. 39. On the left, a shoot of *Acacia cornigera* occupied by a large colony of *Pseudomyrmex ferruginea.* On the right, a shoot of *Acacia chiapensis* that is occupied as an auxiliary-shoot of the colony that has its queen in the *A. cornigera.* The colony contains about 10,000 workers. The *A. cornigera* shoot is just beginning its third rainy season as an occupied shoot. The shoot of *A. chiapensis* appeared to be of the same age. The *A. cornigera* is in flower and has not yet begun strong vertical growth. Photo early June 1964 in an abandoned quarry 1 km west of Temascal.

The founding queen only leaves the thorn to collect Beltian bodies and petiolar nectar. At sunrise founding queens have been observed to collect petiolar nectar until the gaster is greatly distended with nectar and return directly to the thorn from which they came. These thorns contain brood and 0-3 workers. Entire and partially eaten Beltian bodies are commonly found in the thorns with the brood of queens that do not yet have workers. In the 38 shoots in plot J that were dissected (thorns opened) on 25 Apr. 1964 (a.m.) six of the 16 thorns with founding queens and brood (no workers) had a total of 40 Beltian bodies in them. Founding queens that have eggs and no larvae do not collect Beltian bodies. The founding queen makes repeated trips in the early morning and stores the Beltian bodies which are then fed to the larvae during the day. As she develops a physogastric condition she is dependent upon her workers to 1) defend the entrance, 2) enlarge the entrance so that she may occasionally move to new thorns, 3) bring food for her and the larvae, and 4) distribute her eggs and larvae to other thorns and shoots.

In addition to competition between queens causing the loss of very young colonies there is some other mortality to founding queens. Up to one queen per thorn may establish themselves and raise some brood in the thorns of a single shoot. Only one of these becomes the queen of the colony that eventually occupies the entire shoot. A thorn may lose its founding queen to a searching queen many times. Occasionally, moldy or dry queens are found in thorns and sometimes they are accompanied by starving or dead brood. *Crematogaster* and *Solenopsis* workers will drag moribund queens from entrance holes. Predating raids of a very small dolichoderine ant drives all queens from all thorns on the shoot and the brood is lost to the invaders. The very small size of this ant (2 mm long) may be a factor in its ease of entry into the thorns. Salticids cannot get past the queen's head but a spider entering temporarily vacated thorns could capture the returning queen. Dead queens have been found in thorns in the webs of spiders. In the Temascal area, when growing in the sun, shoots with more than five thorns, and without a worker force have not been found that are completely free of founding queens. During the period Jul.-May the percentage of founding queens per thorn drops. There is only a slight rise in the number of other organisms occupying the thorns during this decline in the numbers of thorns occupied by founding queens.

Parathion treatments are effective in removing some founding queens (for the most part when they are foraging for food), but re-colonization is so rapid that it is not possible to determine what percentage. Clipped thorns are not attractive to founding queens though queens are occasionally found in naturally broken thorns. They guard the large hole as if it were a normal entrance but are not successful in raising brood in these thorns. Founding queens in auxiliary-shoots and in queen-shoots have only a very short history due to the constant efforts of workers to remove them, unless the shoot is abandoned during the cool and dry season.

Physogastric colony queen. Even though confined to a thorn when fully physogastric, the colony queen is very agile. On rough surfaces such as paper or the walls of the inside of the thorn, she walks easily, but on the smooth glass tube of a laboratory colony slips occasionally. When newly placed in a laboratory colony she ceases egg laying in 1-9 days, but then when Beltian bodies are made available she begins to lay in 6-12 days. When the physogastric condition is reduced to the state where the gastric sclerites are nearly approximated, she can run freely on a vertical or horizontal sheet of paper.

She holds her gaster in place and above the surface even when running horizontally on a vertical surface. Eggs are extruded by rhythmic pumping of the gaster. It is suspected that the queen ceases egg production 3-4 days before she changes thorns and therefore has a gaster with a reduced diameter when she passes through the thorn entrance. Both of the queens observed while changing thorns were only partly physogastric. When a shoot is cut, the queen is transferred along with the remainder of the colony to whatever living shoots are available (on the cut stump or a neighboring shoot).

No mortality factors have been observed for physogastric queens except fire and other forms of complete colony destruction. Many workers may leave the thorn when the temperatures in the thorn are over 43.5° C.; it is possible that a colony queen could be killed at these high temperatures. When a shoot is cut and placed where there is no access to a new *A. cornigera,* the colony is gradually reduced in size as the larvae die and workers wander off and are lost. The last remnants of the colony are 1-2 thorns with 5-30 workers and the colony queen with a gaster that is only slightly enlarged. However, on one enigmatic occasion, a colony that had been stored in a bare, dry room for 32 days still had 38 workers and one fully physogastric queen. When first cut, this colony had about 1,000 workers.

Behavior of male: Outside of the thorn before copulation. When leaving the shoot, the males' activity is like that of the females but the males fly almost immediately after leaving the thorn. Both sexes may be observed to leave the shoot at the same time. The males appear to fly directly to one of the high points where the females are presumed to be releasing a pheromone. The males always come from the downwind side of the tree (flying upwind). In the area where mating flights were observed, most of the vegetation was low (1-2 m tall) with outstanding objects (telephone poles, palms, occasional broad-leafed trees). The flight pattern of males at daybreak is the following. The males fly to the top of the outstanding object. With a hovering flight they fly around and above any surfaces. The largest concentration is in the area from which the most copulating pairs are falling. An estimated 10,000 males have been seen in the canopy of a single palm. However, most flights are smaller. Many males land on the surface and run up, down, and around in small circles. They buzz their wings continually. If a female is not found, the male continues to fly around the object but he constantly loses altitude. When 1-4 meters from the ground, he flies straight out and away from the site of the swarm in an upwind direction. In this flight he gradually gains height and by the time he gets to the next outstanding object he is back up to a height of 3-7 meters above the ground. The swarming activity is then repeated. One male usually participates in several different swarms in a single morning. As it becomes lighter and warmer in the morning, the number of males swarming gradually diminishes. The swarm lasts until about 30 minutes after the last copulation takes place. This is 15-100 minutes after sunrise.

Whether the morning is clear or cloudy seems to have little effect on the duration of the flight. That the males continue to fly about a site after the females have gone is probably due to attraction to a residual of the sex attractant. Males have only been observed to swarm on high objects on which females were known to be present that morning.

The reduction of the number of males in the swarm is for the most part due to individuals settling on the underside of leaf surfaces where they remain immobile for the rest of the day. They are alert to shaking of the leaves and if disturbed will fly to a new leaf. They are usually 2-5 meters above the ground and often in the same tree in which the swarming took place. That the resting males take part in the next morning's mating flight is substantiated by the fact that at any given swarm, males outnumber the females 100 to 1 or more. Sex ratios in the colonies are approximately even. For how many mornings the male is active is not known.

When the male lands on a surface on which there is a female he usually finds her within a few seconds. It has not been possible to determine if he finds her by sight alone or by odor as well. While males chase each other, copulation attempts between males have not been observed. Once one male is in copula with the female, another may find them and climb on. Occasionally, as many as five or ten males may do this. The only result is that the entire mass usually falls from the surface and breaks apart. Only one male copulates with each female.

At certain times of the year, there is heavy predation of the males. During the dry season, the two vespids, *Stelopolybia areata* and *Polybia occidentalis pygmaea,* are constant predators of male *P. ferruginea* from about 15 minutes before sunrise until the end of the swarm. They are not yet present when the greatest part o fthe mating takes place. On palms, a large flat spider *(Selenops galapagoensis)* is an ever-present predator of the males that alight and is always found feeding on a ball of mashed males. While it feeds, any male that lands nearby is caught. It appears that the two species of vespids take about 200 males per morning per site and the spider about 100 out of a swarm of 500 to 2000 males). *S. areata* flies off easily with a male; they are captured while they are on the leaf surface. The smaller vespid *P. occidentalis pygmaea* often falls or glides to ground level. It may alight and cut the head and wings off the struggling male before flying off. Male head capsules have been found in passerine bird droppings but not as frequently as are workers and queens. They are also occasionally found in the stomachs of skinks, *Anolis* and other lizards.

After copulation. On Jul. 28, 1964, 16 males were observed to fly back up into the swarm after each broke free from a female. This activity was observed on a number of occasions. This indicates that a male may attempt to copulate more than one time.

MORTALITY FACTORS OF WORKERS. Despite the fact that the entire colony is quite concentrated in its living space and foraging range, there is substantial mortality of workers. It is estimated that a four year old colony with 12,000 workers may have produced 26,000 workers during its life. The average rate of removal is probably about one per day for the first year, five per day for the second, ten per day for the third, and 20 per day for the fourth. This rate of loss is not constant throughout the year. A three year old colony may lose 1,000 workers in two hours in a fight with an invading colony (Fig. 40). During the dry season, predation of workers both on and off the shoot by lizards and birds is much more frequent than during the rainy season, when other insect prey is available for these predators. The rate of loss increases as the colony increases in size (age) because the larger the colony, the more workers there are off the shoot; workers off the shoot are much more vulnerable to predators. Further, the larger the colony, the more involved the colony becomes in maintaining auxiliary-shoots; when the connection to an auxiliary-shoot is broken, or when a colony fights over an auxiliary-shoot, there is substantial worker mortality. An age-specific survivorship curve for an even-

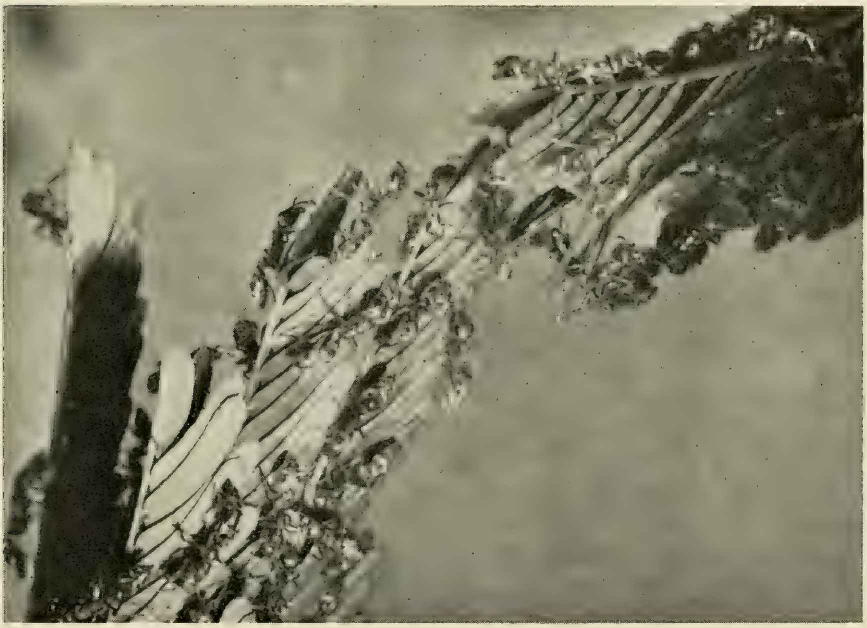


FIG. 40. A point of contact between a branch from a queen-shoot of *Pseudomyrmex ferruginea* and a branch from an auxiliary-shoot from another colony of *Pseudomyrmex ferruginea.* The branches were blown together and held by locking thorns. About one-half of the workers in the photograph are from each colony. While much of the fighting starts when a worker goes from one leaf to the other, many workers pass this area and do not begin the fight until they are 5-50 cm from the point of contact. Most of the fighting workers fall to the ground where they are often eaten by lizards. Photo early May 1964 in plot U.

aged worker cohort is a straight horizontal line until duties outside of the thorn begin. Then the curve should turn downward at an increasing rate as the workers become more aggressive with increasing age.

Fighting. Cleaning and patrolling workers do not hesitate to attack ants from other colonies. When removing a founding queen from a thorn and killing her, the worker is often not killed. When a single worker wanders onto a shoot occupied by another colony, she rarely kills more than one foreign worker before being killed herself. The invading worker is normally the less aggressive of the fighting pair. When the wind blows the branches of two queen-shoots together each colony tries to invade the other (Fig. 40). A group of 500-1000 workers from each colony gathers at the site of branch contact. The leaves and branches are covered with balls of fighting ants, and with workers that are chasing each other. Worker mortality on both sides is very high and the ground is littered with dead, dying, and dismembered workers. The queen of the overpowered colony is killed. How much of the losing colony is incorporated into the winning colony is not known. The same thing occurs when a colony tries to overpower an auxiliary-shoot possessed by another colony. At least 1,000 workers died in the merger of two colonies which afterwards had 3,200 workers.

When a shoot containing a queen-unit colony is cut and laid on the ground near a large queen-shoot, it is not long before workers from the cut shoot find the live shoot. The attempted invasion is usually slow to start and often disorganized with several trails leading to the upright shoot. If the colony in the upright shoot has time to rest, a group of several hundred workers cluster on the bark at the base of the trunk and attack each foreign worker as it tries to go up the trunk. In contrast to the willing and disorganized defense at branch contacts between two colonies, this organized system results in the loss of few workers by the owner colony. The attempted invasion usually stops in a short time.

There is also worker mortality during defense of the colony from other organisms beside *P. ferruginea.* Workers that attack large animals are often carried from the shoot. Occasionally, an insect that is chased from the shoot leaves with a worker clinging to it. These workers do not normally find their way back to the colony. When a normal shoot is invaded by a doryline raiding swarm *(Labidus praedator)* or column *(Nomamyrmex esenbecki),* no disturbance reaction is observed; the workers outside of the thorn become relatively motionless or evasive. The dorylines do not enter the thorns. On shoots with experimentally clipped thorns, dorylines completely clean the shoot of workers and brood, and many workers of *P. ferruginea* die fighting the invading ants.

Wandering. There is a steady flow of a few workers away from the shoot into the surrounding vegetation. It is these workers which are responsible for the discovery of auxiliary-shoots. They are very susceptible to predation (birds, spiders, lizards). In most cases, they probably starve if not eaten, or are killed when invading a shoot occupied by another colony. If they find an unoccupied shoot, then they must repeat the return trip to the parent shoot. Single large workers are occasionally found wandering on shoots that have no unit of brood or workers in them.

Products from the queen. An auxiliary-unit can maintain its organization for at least five weeks without establishing contact with the queen-unit. Colony disorganization following the loss of the queen seems closely related to the maturation of larvae; this occurs when there are no new eggs. There is no evidence of workers laying eggs. As the colony decreases in size, worker mortality rates increase because the workers do not keep predators such as spiders off the shoot. The number of workers present to care for the brood decreases, with increasing appearance of starvation symptoms among the larvae. With decreasing worker density, phytophagous insect damage to the shoot increases, and this reduces the amount of Beltian bodies available for the brood. In the final stages of colony degeneration, only moldy brood remains.

Lizards. The lizard *Sceloporus variabilis,* skinks, and *Anolis* sp., all eat workers of *P. ferruginea* when the workers are encountered on the ground. During the dry season, from 2-44 workers have been found in the stomach and intestine of adult *S. variabilis.* This lizard also occasionally eats ants in the genus *Solenopsis* and other small insects. During the rainy season, this species of lizard also eats *P. ferruginea* workers, but they constitute a much smaller part of the total volume of insects eaten. *S. variabilis* and *Anolis* sp. are not seen climbing on occupied shoots, but they are occasionally seen on unoccupied shoots. Most of the workers that they eat are caught on the ground. *S. variabilis* is often attracted to the ground under fighting colonies where many workers have fallen. Since *P. ferruginea* is the commonest large epigaeic ant in the newly cleared areas around Temascal, and since it is present all year, it is undoubtedly very important in the diet of these lizards.

Birds. In view of the exposed position of workers on the foliage of *A. cornigera,* it is a tribute to the aggressiveness of *P. ferruginea* that bird predation is relatively minor. The barred Ant-shrike, *Thanmophilus doliatus,* will eat workers of *P. ferruginea* from the shoot in which it has its nest. Passerine bird droppings often contain the head capsules of worker *P. ferruginea.* Small warbler-like birds forage in occupied shoots during the cool season, when there are low worker densities outside of the thorns. They eat 1-10 workers per shoot. The Black-throated Oriole, *Icterus gularis,* feeds on the pulp around the seeds in the legumes of *A. cornigera.* This feeding creates a strong disturbance reaction among the ants, and many of the workers are eaten; the gizzard and intestine of a male contained 332 head capsules of *P. ferruginea.*

Arthropod predators. Inasmuch as the colony is concentrated in the shoot canopy, and patrols this heavily, there are very few arthropod predators that enter the canopy to take workers of *P. ferruginea.* Two species of jumping spiders (*Metaphidippus maxillosus, Corythalia* sp.) take an occasional worker during daylight hours but these are generally found only on weakly occupied shoots. At night, an unidentified spider enters the canopy long enough to catch one worker, then drops out of the canopy to feed on her.

Fire. Any fire hot enough to wilt all of the leaves of the shoot kills the colony. No efforts to remove brood or exit from thorns by the workers are seen at this time. However, a fire may only scorch the lower bark and kill the shoot but not the colony. The colony can then move into the new sucker shoots from the root stock.

Drowning. A. cornigera is not found growing close enough to the water so that the canopy will be submerged by the rising river during the rainy season. The submerged shoots are not killed, but the ant colony is. This is especially notable when the river subsides and drowned founding queens are found in the young shoots growing in riverside vegetation. If there is a dry year, the shoot may grow high enough to raise the canopy and its colony above the high water mark, and then the shoot develops normally.

OTHER ACACIA-ANTS IN THE STUDY AREA. Nearly all of the shoots in the study area are occupied by *Pseudomyrmex ferruginea. Pseudomyrmex nigrocincta* and *Pseudomyrmex gracilis mexicana* are comparatively very rare. *P. nigrocincta* is most readily separable from *P. ferruginea* on the basis of the former's paler color, smaller size, and habit of carrying the gaster bent forward under the petiole. In respect to the total population of *A. cornigera* in the Temascal area, *P. nigrocincta* plays a minor role in that there are about 250 colonies of *P. ferruginea* to each colony of *P. nigrocincta.* The same ratio exists in respect to the number of founding queens of the two species. In addition, the two species interact in a very similar manner with *A. cornigera* and *A. chiapensis,* and the same ratio of founding queens is found in the later species of acacia. *P. ferruginea* and *P. nigrocincta* appear indistinguishable in their behavior in harvesting Beltian bodies, collecting nectar, using available thorns for brood, and interacting with other species of ants. They are subjected to the same mortality factors. However, in comparison with *P. ferruginea,* the colonies of *P. nigrocincta* 1) are less thorough and consistent in their patrolling of the shoot, 2) have more timid workers, 3) must grow to a larger size before they provide effective protection of the shoot tips, 4) are more commonly established in shoots that are shaded, and 5) require more time to become reorganized after moving into a new shoot.

There are some significant differences in reproductive biology between these two species. A mature colony of *P. ferruginea* produces a quantity of alates similar to the quantity produced by a colony of *P. nigrocincta,* but a colony of *P. ferruginea* has its first alates 6-12 months before a colony of *P. nigrocincta.* The mating flights of the two species take place around the same high points throughout the year, but the males of *P. nigrocincta* fly slightly earlier than those of *P. ferruginea.* Both sexes of *P. nigrocincta* have been collected at white light about 30 minutes before the slightest visible trace of the sunrise; *P. ferruginea* has not been taken at light. Both species of males may be taken with one sweep of the net in a mating swarm, and mating pairs of the two species have been observed within a few centimeters of each other; it is very likely that the two species recognize their proper females by differences in the sex attractant. About one out of 20 of the new shoots (10-40 cm height range) with founding queens in them has a founding queen of *P. nigrocincta* in one of its thorns. This indicates that there is a mean number of about 12.5 thorns per shoot at the time when one species or the other takes over the shoot. Sufficient information is not available to postulate the reasons why the relative density of the two species is so disproportionate in the study area. As one moves south to Costa Rica, *P. nigrocincta* becomes much more common.

P. ferruginea and *P. nigrocincta* are much more similar in behavior and morphology than either is to *Pseudomyrmex gracilis mexicana.* While the former two species can be regarded as obligate acacia-ants, the later must be treated for the present as a facultative acacia-ant (Wheeler, 1942). In the course of this study, evidence has been gathered that indicates that the apparent intermediacy is due to the existence of several populations which are morphologically indistinguishable but differ in behavior. This aspect of the bionomics of *P. gracilis mexicana* will not be discussed further in this paper, but is under study.

P. gracilis mexicana does not interact with any of the swollen-thorn acacias in the same manner as *P. ferruginea* and *P. nigrocincta.* A mature colony of *P. gracilis mexicana* rarely has more than 1,000 workers. When the colony is living in *A. cornigera,* the thorns that contain brood are usually distributed among 2-15 different shoots. Under natural circumstances, these shoots are usually unoccupied and shaded shoots in the 15-60 cm height range. Taller shoots of all heights are occasionally found with all or part of a colony of *P. gracilis mexicana* in their thorns. These shoots are normally unoccupied by *P. ferruginea* and in very poor condition in comparison with the neighboring shoots that are occupied by *P. ferruginea.* The workers of *P. gracilis mexicana* do not patrol the shoot surface and are only aggressive toward small insects; even in this case, the initial approach to the insect is cautious, and an effort is made to capture the insect. When living in a shoot of *A. cornigera,* a large part of the diet is Beltian bodies. When harvesting them, the worker often chews up the first one and incorporates it into the buccal pellet and then cuts another to carry to the brood. A foraging worker may travel as far as 15 meters between the shoot tip and the particular thorn to which she is returning. The workers clean out green thorns in the same manner as do *P. ferruginea,* but the entrance hole is larger. When the colony of *P. gracilis mexicana* is in hollow branches instead of swollen thorns, the bionomics of the colony is like that of the species of *Pseudomyrmex* not associated with living plants.

Along with ants of the genus *Crematogaster, P. gracilis mexicana* is the common and usual inhabitant of shoots of *A. cornigera* that are unoccupied by *P. ferruginea.* In areas where *A. cornigera* is an abundant plant, *P. gracilis mexicana* is one of the most commonly observed ants foraging in second growth vegetation 1-3 years old.

DISCUSSION. The members of the genus *Pseudomyrmex* can be roughly divided into three groups. Those of the larger group are not associated with any particular species, or group of species, of living plants. They live for the most part in hollow, dead stems and the colony is occasionally extended into the pith canal of a living stem. The adults feed on nectar from plants (floral and extra-floral nectaries) and/or the juices from dead insects and captured living insects. Both living and dead insects are taken as prey by workers foraging individually; this prey is used for food for the larvae. The members of the smaller group of *Pseudomyrmex* regularly live in association with a particular species, or group of species, of living plants. They live in spaces that are in the living plant (e.g., hollowed pith canals) or directly attached to it (e.g., swollen stipular thorns). They depend on modified structures of the plant for part or all of their food (e.g., Beltian bodies), or rear coccids within the hollowed pith canals.

Pseudomyrmex ferruginea, Pseudomyrmex nigrocincta, and *Pseudomyrmex gracilis mexicana* are the commonest members of the smaller group within the study area. The former two species live only on/in swollen-thorn acacias, and are quite distant from the larger group in their behavior and ecology. *P. gracilis mexicana* may be intermediate between the two groups.

Like the other species of *Pseudomyrmex* associated with living plants, *P. ferruginea* possesses a number of behavioral and ecological traits which appear to be associated with its interaction with its host plant. However, it also has many behavioral and ecological traits in common with the members of the genus that are not associated with living plants. To demonstrate this, the following list is presented. Each trait is to some degree common to almost all members of the genus.

1) The workers are fast runners, are extremely agile, hold themselves close to the substrate on short legs, and rarely fall off the substrate.

2) With their large compound eyes, the workers are able to respond to moving objects up to distances of at least 1 m. Up to a certain point, the faster an object is moving the more likely it is that the worker will show a response.

3) While the portion of the colony occupying a single shoot functions as a unit due to the summation of the members' activity, each individual worker acts relatively independently of the other workers when outside of the thorns.

Workers do not co-operate directly with each other in performing duties outside of the thorns and apparently act normally when separated from the other workers.

4) The workers and alate females have a well developed barbless sting with a barbed sting sheath; they do not hesitate to use it on any animal that contacts them. Some of the *Pseudomyrmex* that are not associated with living plants are somewhat reluctant to use their sting, or else the worker cannot penetrate the skin or integument of the attacker.

5) The workers frequently lick the surfaces on which they are walking, and what is licked up is incorporated into a buccal pellet; this is in turn fed to a larva. There is no evidence that any solid food is eaten by the workers.

6) The prey (the Beltian body) is brought back to the swollen-thorn without cutting it up or incorporating it onto the buccal pellet. It is then cut into large pieces which are fed to the larvae without further preparation. (Some of the larger species of *Pseudomyrmex* will incorporate small pieces of prey directly into the buccal pellet).

7) When a source of nectar is found, the worker drinks until the gaster is partially distended and then returns to the colony to regurgitate the fluid. Apparently, no effort is made to lead other workers to the source of nectar. A particular worker is quite capable of returning to the same food source if it leaves voluntarily or is chased away. At times it uses an odor trail but at others it appears to use visual orientation.

8) The entrance hole to the living space is cut out by the workers and then masticated wood pulp is laid down by the workers on the walls of the entrance antechamber; this narrows the opening to match the diameter of the worker's head.

9) In the advent that a nest structure is partially damaged or rots, the workers seek a new one and move the contents of the old into it. The larvae are carried one at a time, held straight out in front of the worker. Rarely two workers will both carry a very large larva or pupa at the same time. Workers are carried as well.

10) The living spaces are relatively tubular in form and carton partitioning structures are not produced. There is one entrance to the living space (some species of *Pseudomyrmex* have more than one entrance to the living space).

11) The colony is arboreal. (Some species of *Pseudomyrmex* live at ground level and it is commonplace to find workers of some species of *Pseudomyrmex* apparently foraging on the ground litter. However, they also fall from the foliage and so presence on the ground does not demonstrate that they are foraging there.

12) Except when small enough to fit into one living space, the colony is distributed throughout a number of discrete units. In the case of *P. ferruginea* and other *Pseudomyrmex* associated with living plants, these units are

grouped at a second level, the individual shoot (e.g., the auxiliary-shoots and queen-shoot). A single unit of a colony of a species not associated with living plants often holds a larger part of the colony than does a swollen-thorn, for example, but the units are generally more widely distributed (e.g., in several different plants and vines). The units in all cases are connected by open air paths which may or may not be odor trails.

13) Distinct morphological worker castes are not present and apparently associated with this, each worker probably performs all of the duties in the colony at some time in her life span.

14) The colony has one physogastric queen located in the same unit with most of her eggs. She is agile, attempts to hide when the living space is broken open, and even may attempt to sting. Founding queens are killed by the workers that can catch them. (There are several species of *Pseudomyrmex* which have more than one physogastric queen per colony.)

15) The founding queens use empty living spaces excavated by other ants or insects in plant stems, or if these are not available, they excavate their own. More than one queen cannot found a successful colony in the same nest cavity, except when there is more than one physogastric queen per colony. The founding queen forages food for herself and her brood, until at least several mature workers have been produced.

The following list of traits of *P. ferruginea* contains those which are in some way associated with the interaction of the ant with swollen-thorn acacias. It is in the expression of these traits that *P. ferruginea* demonstrates the greatest differences between it and the species of *Pseudomyrmex* that are not associated with living plants in an obligate manner.

1) A large proportion of the workers in a mature colony are very aggressive toward animals of all sizes that contact the substrate containing the living space (a swollen-thorn acacia). These workers both bite and sting the animal, and only a very few of the very small and soft bodied insects are captured as prey. In contrast, those species of *Pseudomyrmex* that are not associated with a particular species of plant are usually not aggressive towards animals on the substrate containing the living space; even when the nest is broken open they often flee without attacking.

2) Many of the workers in a large colony will maul any vegetation that is not a part of a maturing swollen-thorn acacia, and contacts the shoot or grows in a circular area under the shoot. There is no evidence that the workers of species not associated with living plants chew on plant matter except when excavating a nest site or in some cases, gathering food.

3) The workers of *P. ferruginea* have an especially well developed sting which can penetrate more deeply into human skin than can that of any of the other 29 species of *Pseudomyrmex* collected in the study area.

4) When the weather is clear and warm, the workers are active outside of the thorns both day and night. The workers of species not associated with

living plants have not been collected outside of the nest after dark, and usually they are not present during the early morning and late afternoon hours as well. The workers of *P. ferruginea* are active outside of the nest (thorns) during much more inclement weather than are those of species not associated with living plants.

5) When the weather is clear and warm, from 2-25 percent of the workers are active outside of the thorns, and they are for the most part concentrated within the confines of the shoot. During the daylight hours, equivalent numbers of workers of species not associated with living plants may be outside of the nest. However, they are not concentrated in the immediate area of the nest. In addition, since the colony is often broken up into several widely dispersed units, the workers are even further dispersed. It is only when the living spaces and the food sources are concentrated in a small area (the swollen-thorn acacia), that large numbers of workers can be found outside of the nest yet in its immediate vicinity.

6) On the surface of the shoot, workers often chase each other and only those workers that are carrying brood or prey (Beltian body) dodge away from these attacks. When a worker avoids or backs away from another worker, it is often only after direct contact. The workers of species that are not associated with living plans usually see other ants at distances of 2-15 cm and often dodge away from them.

7) When on trails between shoots, the workers appear to be strongly dependent upon odor trails for orientation. The workers of species not associated with living plants use both visual and odor orientation when traveling between the parts of the nest.

8) The colony may attain a very large size (12,000-plus workers) and when it is split up into auxiliary-units and a queen-unit, it is composed of several large segments, each of which acts very much like a separate colony. While the size of colonies not associated with living plants is very difficult to determine due to the dispersed placement of the parts of the colony, it is certain that these colonies only rarely attain such a large size; they usually have 500-5,000 workers.

9) Almost the entire colony is confined to a small volume of space in respect to foraging and the situation of the total nest. Workers of species not associated with living plants will forage at least 30 meters from their fraction of the nest, and the parts of a nest may be scattered over an area of at least 300 m^2.

10) Not only is the colony supplied with a continuous food source (though a fluctuating one), but it is also continually being supplied with new nest sites, except during the dry season. The result is that the colony grows much more rapidly than does a colony of a species that is not associated with living plants.

11) At a given site, the presence of a colony of *P. ferruginea* is completely dependent upon the presence of a living swollen-thorn acacia. Those species not associated with living plants are not dependent upon the presence of any particular species of plant for their existence. There are certain species of plants which characteristically have hollow branches, but these species of *Pseudomyrmex* may nest in any of them.

12) While the colony is dependent upon the presence of a swollen-thorn acacia for its existence, the fact that a mature colony exists and produces founding queens implies a high probability that there will be seedlings of the swollen-thorn acacia present for the founding queen to settle in. The presence of a colony of a species not associated with living plants does not increase the probability that there will be nest sites available for the founding queens from that colony.

13) As a species, *P. ferruginea* has the opportunity to increase the probability that it will continue to exist by evolving behavioral traits that insure the continued growth and reproduction of the swollen-thorn acacias on which it lives. There is little that a species not associated with living plants can do to insure the existence of sufficient nest sites and food.

14) In man-made disturbance sites, and to some degree in natural disturbance sites, *P. feruginea* maintains a higher density of colonies, and a higher density of individuals, per unit volume of plant community than does any species of *Pseudomyrmex* not associated with living plants.

15) The founding queen does not have to forage more than a few centimeters from the thorn for food for her brood. Since the thorn is on a living plant, she is insured that there will be food within a short radius. A founding queen of a species not associated with living plants must forage long distances from her nest site, and is not insured of finding food.

16) Because of the concentration of the colony in a small volume, and the aggressive behavior of most workers to intrusive organisms, the majority of the members of the colony are not subject to predation. The workers of a colony not associated with living plants are preyed upon whenever they leave the nest.

It should be evident from the above comparisons of *P. ferruginea* with other ants in the genus *Pseudomyrmex* that *P. ferruginea* is more than just an incidental tenant in the swollen thorns of *A. cornigera* and the other swollen-thorn acacias within its range. Behaviorally, *P. ferruginea* is highly adapted to living on swollen-thorn acacias—so much so that it is not found elsewhere. However, this is not a one-sided interrelationship. *A. cornigera* is likewise highly adapted to the presence of the ant; this aspect of the ant-acacia interaction is presented in the third section of this paper. It should be noted that in both the ant and the acacia populations, the most important changes that are associated with the interaction are primarily behavioral and physiological, rather than morphological. As such, they are often much less clearly distinct from similar but different traits of the ants and acacias that do not have an interaction with each other. The evolution of this system is discussed in more detail by Janzen (1966).

FACTORS INFLUENCING THE PARAMETERS OF *ACACIA CORNIGERA* POPULATIONS

A swollen-thorn acacia is necessary for the development of a colony of *Pseudomyrmex ferruginea.* This is evident from the previous information of the bionomics of the ant. It is likewise evident that the behavior of *P. ferruginea* is modified from those species of *Pseudomyrmex* that are not associated with a living plant. This modification appears to be in a direction such as to facilitate the association of *P. ferruginea* with a swollen-thorn acacia. Earlier authors (Belt, 1874; Brown, 1960; Schwarz, 1916; Wasmann, 1915, 1916; Safford, 1922; Schimper, 1888) expressed the belief that the ants protect the acacia (in general reference to New World swollen-thorn acacias and *Pseudomyrmex*). Preliminary observations during the summer of 1962 at Campo Cotaxtla suggested that some important population parameters (height, condition) of *Acacia cornigera* are influenced in a positive manner by the presence of *P. ferruginea.* Often, this influence is not immediately apparent by casual observation. Therefore, the majority of the experimental work in this study dealt with attempts to gather data to reject the null hypothesis that the absence of a colony of *P. ferruginea* has no effect on the population parameters of *A. cornigera.*

Other authors (Skwarra, 1934a; Wheeler, 1913, 1942) have expressed the view that the ants do not protect the acacia. Difficulty undoubtedly arises over the word "protect." Most of the confusion has arisen through the failure to observe specific phytophagous animals and to record their effect on the shoot, and the effects of the ants on them. An equal confusion has arisen from the desire of most authors to develop a single hypothesis which covers all interactions of an apparently mutualistic nature between ants and living plants. Whether or not a mutualistic relationship exists between a given species of ant and plant is completely dependent upon the behavioral and ecological characteristics of the particular ant and plant species. Until many more ant-plant interactions are investigated in detail, it is premature to attempt general hypotheses that are concerned with the presence or absence of a mutualistic relationship. Observations made external to the interaction between *P. ferruginea* and *A. cornigera* indicate that the interaction is at least quantitatively, if not qualitatively, different from many other interactions between a species of *Pseudomyrmex* and a species of *Acacia.* Extreme care must be used when using the data presented in this paper to develop hypotheses bearing on the existence of a mutualistic relationship between other species of ants and plants.

Materials and Methods

Study area. The major part of the experimental data in this paper is from the same site as the data presented in the sections on *Acacia cornigera* and *Pseudomyrmex ferruginea.* The experimental plots (1963-1964) on the land of Senor Eusavio Farfan (4 miles east of Temascal), and Juan Torrealva (7 miles east of Temascal), are within 1,000 meters of the highway between Temascal and La Granja (Fig. 7). This is lowland coastal plain 2-22 km east of the first foothills of the Sierra Madre Oriental, at an elevation of 15-40 meters. Plot B is on the dam fill and waste land along the west side of Temascal, and therefore in the foothills. The initial experiments and observations were recorded from the lowland coastal plain immediately surrounding Campo Cotaxtla. To aid in the comparison with further studies, the following characteristics of the part of the study area containing the experimental plots are presented.

Soils. Unless otherwise indicated in the individual plot descriptions, all experimental plots are on black soil with limestone outcrops, or on red to yellow laterite with quartz pebbles. Nothing is known of the relation of the distribution of *A. cornigera* to these two soil types prior to man's intervention in the area. At present, *A. cornigera* is common on all black soil areas except where the land is burned and/or plowed annually, flooded annually, or covered with forest that has not been disturbed for 9-20 years. The low laterite hills are covered with oak, *Byrsonima crassipes, Curatela americana,* grasses, and other fire-tolerant plants. They are usually burned every 1-3 years. *A. cornigera* is absent on these hills but once fires become less frequent due to conversion of the site to a pasture or corn field, *A. cornigera* becomes common. There are no obvious major differences between the density or distribution of *A. cornigera* that are directly attributable to the diffferent physical or chemical properties of these soils, although under the same disturbance regime, *A. cornigera* may not be as common on the drier laterite as on black soils. However, the growth of other plants on these soils influences their use by man and this does affect *A. cornigera* density and distribution. The two soil types have about equal acreage in the area between Temascal and La Granja.

Precipitation. Rainfall data were obtained from unpublished and published (Comision del Papaloapan, 1962) reports from the Comision del Papaloapan weather station that is situated on a hill (elev. 80 m) overlooking Temascal. The amount of rainfall, and its periodicity, recorded at this station closely approximately that observed in the plots. The same rain squalls that passed over the plots usually passed over the weather station, although 10-120 minutes later.

At Temascal, the 12 year (1951-1962) mean annual precipitation was 282 cm (range 158 to 372 cm). In 1963, there was 198 cm of precipitation. The first heavy rain in 1963 was on 7 May (66.2 mm). From this date to 25 Sept. 1963, the date of the last heavy rain (25.3 mm), there was 183 cm of precipitation. From 26 Sept. 1963 to 19 May 1964 there was 6 cm of precipitation. The first heavy rain was on 20 May 1964 (18.5 mm). From that date to 8 Aug. 1964, there was 129 cm of precipitation.

On the basis of these data, it is easy to define the beginning of the rainy season as the date of the first heavy rain (7 May 1963 and 20 May 1964). In 1964, there was 3 cm of precipitation in the 49 days preceeding 20 May. During the 49 days following 19 May, there was 94 cm. Within two weeks after the beginning of the rainy season in 1964, the soil was soaked, and patches of ground that had been bare during the latter part of the dry season were covered with seedling plants. Mature plants were slower to show a reaction and only near the end of June did most species have branches in full leaf. The general density of insects in the vegetation was relatively slow to increase and did not appear to reach usual rainy season levels until the end of June. There were, however, some species which made their appearance in large numbers 1-3 days after the 20th of May. Seeds of *A. cornigera* began to germinate almost immediately after the first heavy rain and continued to germinate sporadically for at least two months. Those mature shoots of *A. cornigera* that were in flower took as long as two months after the first heavy rain to initiate lengthening vertical branches. Some sterile shoots initiated vertical growth anytime after the cool season ended (early March) but most of the shoots initiated vertical growth in the month preceding, and the six weeks following, the beginning of the rainy season. Aside from those specific defoliators of *A. cornigera* which were present throughout the dry season, (*Coxina hadenoides, Aristotelia corallina*), insects that eat *A. cornigera* did not appear in numbers until the first week after the first heavy rain.

Defining the end of the rainy season (and the beginning of the dry season) is considerably more difficult. The date of the last heavy rain in 1963 was 25 Sept. (3 cm). This is chosen as the end of the 1963 rainy season. Thereafter until 20 May 1964, rainy days were separated by rainless periods of 1-25 days. When rain did fall there was rarely over 0.5 cm. The reduction of plant growth rates and insect density during the first part of the dry season was intensified by three months of cold weather which began about 1 Dec. This is regarded as a cool season (Table 3) and is included in the dry season. When temperatures rose in March, there were few species of plants which initiated heavy growth. The point at which different plant species drop their leaves ranges from early December to the middle of April. The largest portion of deciduous plants drop their leaves shortly after the end of the cool season. However, this refers only to those shoots that are over 6-10 months old. Younger regeneration shoots of many species of trees and shrubs retain their leaves in large part; pastures cleared within the past 6-10 months stand out clearly against the surrounding brownish gray and leafless vegetation.

The shoots of *A. cornigera* are variable in respect to their reaction to the beginning of the dry season. Those that are growing in areas where the water table is close to the surface (swamps, river banks) lose their leaves and cease growth later than do those growing in better drained sites. In some cases, *A. cornigera* is sometimes the only plant with green leaves except for much larger trees. Flowering branches are often initiated during the dry season and sometimes extended the height of the shoot by 10-30 cm. However, these branches do not lengthen more than this; the new vertically lengthening sterile branches are initiated from a thorn axil at the base of or below the flowering branch. Even when the shoot has an undamaged shoot tip, its rate of growth during the cool and dry season is somewhat lower than during the rainy season.

Temperature. Temperature data were obtained from the same source as the rainfall data. This station records the daily maxima and minima. The minima agreed very closely with those occasionally recorded in the plots. The maxima were 1-4° C. lower than those recorded in the plots on those days when the maxima were above about 32° C. It can be seen from Table 3 that there is a readily definable cool season that lasted approximately three months, December through February. The lowest temperature recorded in the experimental plots during the cool season was 10.5° C. at 4:00 a.m. on 26 Dec. 1963. The high number of days (40) with a maximum of 24° C. or less during the cool season was of great significance to *A. cornigera* and *P. ferruginea*. When the maxima are less than 24° C. there are almost no workers active on the surface of the shoot throughout the entire 24-hour cycle.

Two types of cool weather occurred while the study was in progress. When storms blew from the Gulf of Mexico, they brought wind and rain with diurnal temperature maxima in the 22-25° C. range. Nocturnal temperatures usually did not drop below 15° C. during these *nortes*. During the cool season there were frequent storms with very light rain or drizzle and overcast skies. During these periods, diurnal maxima ranged from 16 to 23° C. and nocturnal lows ranged from 10.5-19° C.

On clear days during the warm season, temperatures at sunrise were usually 21-24° C. They climbed rapidly after sunrise (e.g., from 22° C. at 6:00 a.m. to 30° C. at 9:00 a.m.) and fell rapidly at sunset (Fig. 32, 33). On overcast days, maximum temperatures were sometimes less than 4° C. higher than those at dawn. On clear days during August through November, a heavy morning fog was often present until 7:00-9:00 a.m. This kept temperatures low until the sun broke through.

Aside from the records of the weather stations of the Comicion del Papaloapan, all air temperatures were recorded with a Yellow Springs Instrument Company Model 44TD telethermometer and probes (#402 Small Animal Probe). Over the range of the scale that was used, these probes read within less than one-half degree C. of each other and a calibrated mercury thermometer. Unqualified statements about air temperatures refer to that recorded 1 m above open ground with the probe and lead in full sun and wind for about 30 seconds. When measuring the temperature inside of small shaded sites (e.g., in thorns), at least 50 cm of the lead immediately adjacent to the probe was also shaded. The probe was placed in the thorn by clipping off the point lacking an entrance until the hole was just large enough to admit the probe. In occupied thorns, the workers chewed the plastic coating off of the probe on numerous occasions.

Land use. The La Granja-Temascal highway was built about 1950. Before this, the area was used for milpa agriculture by Indians and contained several small holdings used as brushy pasture (e.g., Señor Farfan's land). Upon opening to settlement and the relocation of eight Indian villages evacuated from the lake site behind the Presa Miguel Aleman, farming became more intensive, and grazing pressure by cattle increased. Every year, more land is converted to sugar cane fields.

Plot B at the base of the earth-rock-fill dam is on sandy soil and in open, heavily grazed and browsed vegetation. Throughout the study area, *A. cornigera* is common on this type of land.

.The experimental plots on Señor Farfan's land (F-I, K, N-Q, S-V) are in second growth natural vegetation which is subject to periodic grazing, clearing and/or burning. Whenever funds are available, the owner has portions of the brushy pasture cleared. If the litter dries it is sometimes burned. From 3-36 months may elapse between clearings and/or burnings. This process results in a closed (lightly grazed) to open (heavily grazed) plant community composed mostly of annuals and suckers from old perennial root stocks. The annuals set seed every year but the suckers often require 2-4 years of growth before setting seed.

On Señor Torrealva's land (the remaining plots) the vegetation is subject to alteration by farming and grazing. In general a sector is cut and/or burned in April or early May. It is then planted to corn without being plowed; certain portions receive beans and squash as well. Following corn harvest, and the later squash and bean harvest, cattle are allowed to graze the area until the following spring. This cycle is repeated at least three consecutive years and then the land is left fallow for 2-5 years. This land receives light to very heavy cattle grazing while fallow. During the fallow period, the vegetation may be cut and/or burned at irregular intervals to provide new suckers for fodder.

At Campo Cotaxtla, almost all experimental work was with shoots over a year old in short-grass pasture and brushy pasture.

Vegetation types. The coastal plain immediately east of Temascal is Tropical Tropical Dry Forest based on climate and altitude (Holdridge, 1964) or Tropical Tropical Evergreen Forest based on climatic factors and an appreciation of the vegetation itself (Leopold, 1959). The plot B at Temascal was the only one within eight km of forest over 20 years old. The small amounts of this older forest remaining are on the black soil and limestone hills, 150-300 m tall, west of Temascal and bordering the lake behind the Presa Miguel Aleman. The vegetation in and around all plots was cut and/or burned at least once every 10 years and usually more frequently. It appears that before man, two plant formations may have been recognizable; one on the low laterite hills, and the other on the high hills and bottomlands having black soils. No attempt will be made to characterize these earlier formations. Man's disturbance has been so great that it is nearly impossible to say what plants lived in what areas and at what densities. Almost all of the species of plants in the area appear to have their densities and distributions altered by man's disturbance.

At present, the low laterite hills have the following four types of vegetation. (1) Grassland that is burned annually with herbaceous annuals and scattered fire-resistant trees. (2) Grass with shrubs 1-2 m tall, and more dense trees that form a nearly closed canopy in some places. These sites are burned every 2-3 years and are not used for intensive grazing or farming. (3) Dense shrub layers of Compositae, Leguminosae, Melastomaceae, and other plants with root stocks resistant to burning and plowing. These are tied together with vines which have perennial root stocks, and are under scattered oaks, palms, *Ateleia pterocarpa, Cochlospermum vitifolium, Byrsonima crassipes* and other trees. This vegetation is burned and cut periodically for conversion to corn fields, with or without grazing. (4) A closed canopy of *Quercus*, Leguminoase, Melastomaceae and other trees with woody vines in the canopy. This forest is 10-18 years old, gradually loses its undershrub layer and is not burned except by very light ground fire.

These four patterns can be, and are, modified in all directions and to all extremes by grazing, lumbering, and clearing *para ver mas lejos* (to improve the view). In type (3), *Acacia cornigera* may become very common provided the land lies fallow without burning for at least three consecutive years during each six years of use. *A. cornigera* is generally absent in the other three and this appears to be associated with the frequent burning of types (1) and (2) and the dense shade of type (4) during the rainy season. Plots D, J, and R are in the successional stages of type (3).

The areas of black soil with limestone outcrops have received very different treatment in past years due to their superior value for corn fields and pasture. Even under these conditions of extreme disturbance there are certain plant species which are noticeably lacking from one or the other soil types. Furthermore, it appears that a similar disturbance regime does not always result in the same vegetation physiognomy on the two soils.

The disturbance regime of the vegetation on black soil is so complex and so compounded by cutting, burning, grazing, and establishment of fallow lands, cornfields, and cane fields, in every imaginable sequence, that a classification even as crude as that for the laterite soils is unreasonable at this point.

In ungrazed regeneration following cutting and/or burning, the plants are characteristically 1) uniform in height within the species, 2) of 100 species per acre or more, 3) slender, 4) sprouted from old rootstocks or are annual herbs and vines, 5) reactive to the dry period by leaf-drop and cessation of vertical growth, 6) woody, 7) entangled by woody and annual vines, and 8) with a species density and composition that changes from year to year (succession) and from area to area (disturbance regime). *A. cornigera* is often common in such regeneration as suckers from old root stock. Plots E, C, H, I, K, N, O, P contained vegetation of this type that has been lightly to moderately grazed until the beginning of the 1964 rainy season when the cattle were removed.

As grazing pressure increases, the vegetation structure deviates from this description. Regeneration of natural vegetation during or immediately following heavy cattle or horse grazing is characterized by 1) lack of uniformity in height within many of the species, 2) reduced species composition (as low as 25 species per acre), 3) many plants laterally developed or with stag-horned life form, 4) annuals or plants grown from old root stock, 5) asynchronous leaf drop between species, 6) plants with thorny, bitter tasting, hairy, or urticaceous foliage, and/or stinging ants, 7) being much less tangled with woody vines and almost lacking annual vines, 8) lacking a closed canopy above the grass level, 9) having many grasses and, 10) lacking a great change in species composition on a yearly basis (succession) and area to area basis (disturbance regime).

The degree of divergence of this type from the one previously described depends for the most part on the time of year when the last clearing took place, intensity of grazing, and the time of year the grazing occurred. In this last type, *A. cornigera* is often very common. Plots L, M, Q, and S were of this type.

Sugar cane fields, owing to their annual cutting and burning, and the dense shade and root competition produced by the tall grass formation, are relatively barren of anything other than root stocks with suppressed shoots, and herbaceous annuals (e.g., Convolvulaceae). Shoot densities of *A. cornigera* are very low and *A. cornigera* is usually absent in fields that have been used for sugar cane for more than five years. When fallow they approximate ungrazed regeneration following cutting and burning for a corn field.

An almost complete disappearance of natural vegetation occurs when the land is completely cleared and planted to a vigorous grass species. If such a pasture is not burned more often than biennially, vigorous stands of *A. cornigera* may develop and remain. The plots established in a pasture of this type were accidentally destroyed.

Choice of plots. Plots were generally chosen in areas with moderate to high densities of *A. cornigera.* See Figure 7 for the location of those retained in the study. Early in the study, attempts were made to establish lines of shoots as linear plots. Owing to difficulties in marking shoots, difficulties in explaining to land-holders what was desired, and a lack of understanding of the auxiliary-shoot effect, these plots were found to be impractical at the time and were abandoned. Rectangular plots were then used. Each plot has a single disturbance regime; in some cases several plots were established in a field that had a uniform disturbance regime throughout. The various portions of the plot that are altered, treated or used as controls are designated as "subplots." Rectangular subplots could be readily outlined, eliminating bias of which shoots to treat since all *A. cornigera* in the experimental subplot could be treated equally. They could be described more readily, and provided large samples without intricate mapping. As the study progressed, difficulties with the placement and form of these subplots became evident, such as mapping difficulties, inclusion of nonrepresentative shoots, and trails between shoots across the subplot borders, but these problems can be avoided. Linear plots were also used again after the auxiliary-shoot phenomenon was understood (plots B, G, I).

The presence of a population of *A. cornigera* of an age and form desired for treatment was the first prerequisite for the choice of a plot. Of equal importance was permission for, and acknowledgment of the plot's presence by the owner. Some assurance had to be obtained that the plot would not be cleared or burned before August 1964. This permission, acknowledgment, and/or assurance was impossible to obtain for most land in the area between Temascal and La Granja. In spite of having obtained these assurances, 20 plots were destroyed during the study; they were not included in the plot description below. The futility of experimenting with single shoots in small or marginal habitats was associated with these reasons as well as with the high variation between the shoots in these habitats. However, with this study as background, it would now be possible to experiment with the *A. cornigera* growing in such habitats. The above mentioned difficulties are in great part responsible for the lack of replication of subplots. However, in most subplots, each shoot was a replicate in itself since a record was kept of each individual for at least part of the history of the subplot.

Plots were chosen so that they contained approximately even-aged shoots of *A. cornigera.* In special cases certain age or height groups were removed or not recorded in order to create an even-aged stand. These cases are so indicated in the plot descriptions. Care was taken to choose plots that included an area with only one history of disturbance. This history was determined by owner opinions, extrapolating from nearby vegetation with a known history, and the number of annual growth rings in the trunks of *A. cornigera.* The presence of fields, pastures, and roadsides with uniform favorable histories of disturbances has resulted in much larger areas with uniform populations of *A. cornigera* and *P. ferruginea* than could have existed before man's presence, and this has simplified experimentation with these two organisms.

Treatments. Insecticide. At Campo Cotaxtla in July 1962, it was found that two methyl-parathion sprays applied a month apart were effective in removing colonies of *P. ferruginea* from 2-4 year old queen-shoots; upon re-examination of these shoots in September 1963, it was found that 18 of the 23 treated shoots completely lacked workers. The spray used was a 0.03 percent emulsion of 50 percent actual, liquid concentrate Beyer Leverkusen methyl-parathion.

At Temascal, a 0.04 percent emulsion of the same insecticide was used. It was applied with a back-pack sprayer with a 2 m extension boom until the foliage and bark were wet. Care was taken to spray both sides of shoots. A "Spraying Systems C. Tee Jet TG-5" medium fine spray nozzle was used. This application required approximately 35 cc per 30 cm shoot. 400 cc per 160 cm shoot, and 1,000 cc per 400 cm shoot (determined by matching mean volumes against mean heights in three subplots). At least 50 percent of the spray mixture fell directly on the foliage of other plants but almost none fell directly on the ground, except when other vegetation had been cleared. Spraying was done when the wind speed was 2 mph or less in order to minimize drift onto control subplots and reduce foliar contamination of other plants. Shoots were not sprayed when wet with rain or dew. This meant that spraying was almost always done from 8:00-10:30 a.m. and 3:00-6:00 p.m.

The original schedule was two applications about a month apart on each treatment subplot during the fall of 1963. The fisrt application was expected to remove most of the adults and larvae while the second would kill those workers that had hatched from unaffected pupae during the intervening month. In order to avoid mortality to defoliators at the time when most of the shoot growth occurs, no applications were planned for the 1964 rainy season. After this schedule had been followed for most of the treatment subplots (through Dec.), it was decided that a more satisfactory technique should be used. This was for the following reasons. 1) Sprayed shoots were still available for founding queens and these would have small but active new colonies by June of 1964. 2) Unoccupied shoots in the treatment subplots frequently were invaded and became auxiliary-shoots of large colonies along the plot margins. 3) A few workers (5-100) sometimes remained for a month or more after the last spray application and could affect defoliating insects coming to the shoots. 4) In one case an entire queen-unit moved into the treatment subplot and into a shoot emptied by methyl-parathion mortality. 5) Spraying removed phytophagous insects for an undetermined period, and it was found that the feeding of even one or two such insects could have a major effect on the population of *A. cornigera.* 6) In some cases there was evidence that the methyl-parathion stimulated growth of *A. cornigera* for a short period of time after each application.

After a shoot was sprayed, the workers were often seen turning in tight circles on the surface and then falling off the shoot. These workers cease movement in 5-10 minutes. Larvae that were dead due to contamination from workers were thrown from the shoot in large numbers. Workers appeared not to die in the thorns but it is more likely that they were thrown from the thorns like the dying larvae. The queen was usually killed within three days after the first treatment. The dead queen was not pulled out of the thorn.

Two examples of the effectiveness of treatment with methyl-parathion are as follows. 1) Nine days after the second spray in treatment subplot SA-1 (later abandoned), 2,105 type A and B thorns from the area of brood thorns of 17 shoots were opened. Of these thorns, 43 still had unstarved brood and workers, 351 had starved or moldy brood, and the remainder had workers only or were empty. Before the first spraying there were probably brood in at least 90 percent of these thorns. By July 1964, the shoots along the north margin of subplot SA-1 appeared to be fully occupied as auxiliary-shoots of the colonies in control subplot SA-2. 2) On 21 Jan. 1964, 61 days after the second spraying of subplot U-1, 175 workers were counted on the outside of the 86 shoots in the treatment subplot U-1 and 2,219 workers were counted on the outside of the 93 shoots in the control subplot U-2.

Two days after a single spray application, ten unoccupied shoots (20-40 cm tall) had 21 percent of the thorns tenanted by founding queens. However, four days later, ten more shoots from the same site had 87 percent of the thorns occupied by founding queens. This latter level is about the usual frequency of founding queens. Since the first queen to occupy a thorn on an unoccupied shoot is not necessarily the one to develop the owner colony, spraying to prevent colony foundation is a useless procedure unless done so frequently that it would probably have devastating effects on the other insect populations. In addition, such a treatment could have major direct effects on the growth rates of the shoots.

The effect of the spray application on phytophagous insects could be very important but was not of great concern for the following reasons. 1) The subplots were so small that insects could rapidly reinvade them. 2) It was expected that the major part of the defoliation would take place during the first three months of the 1964 rainy season rather than immediately following the removal of *P. ferruginea* at the end of the 1963 rainy season. 3) It was hoped that methyl-parathion, being a compound with a short half-life, would be gone within a month after the last application.

With the exception of *Sysphinx mexicana,* all of the insects listed in Table 1 are killed by an application of methyl-parathion. This was determined by finding dead individuals on the shoot and on the ground below the shoot. It is not known how long after an application the residual affects the insects that land on the shoot. Dead insects are commonly found under the sprayed shoots only during the first 2-4 days after the application. Severe defoliation may take place on the first day following the application (and on any later date) but it is not known how many of the defoliating agents are killed. Within two weeks after an application, the numbers of phytophagous insects on the shoots were about as high as they were at any time. In both control and treatment subplots, almost all phytophagous insects disappeared during the Jan.-May cool and dry season. Of those insects that feed commonly on unoccupied *A. cornigera,* only *Coxina hadenoides, Coscinoptera mucida, Aristotelia corallina,* and *Mozena tomentosa* remained active at this time. No insecticides were used after the 15th of December.

Methyl-parathion stimulation. In plots with shoots 2-4 m tall, the second parathion application was found to stimulate growth of the upper axillary buds. For example, for 2-6 weeks following the second application (4 Dec. 1963), lengthening branches were evident from the upper thorn axils in treatment subplot S-1. This was at a time (Dec. and Jan.) when the shoots in the control subplot showed almost no new growth. Along the north side of S-1, the treated shoots were less than 1 m from the untreated shoots. This new growth may have been in part due to insecticide mortality of phytophagous insects. In the control subplot (S-2), katydids (Tettigoniidae) and the larvae of *Coxina hadenoides* were responsible for the lack of new growth (in addition to physiological slowing of growth due to the cool weather). These insects are very mobile. Both of these insects were present at the time the new growth was being produced. Due to the cool weather, there was little activity outside of the thorns at this time and these insects were also present in the control subplots. Their characteristic feeding damage was abundant on these new branches. It appears that the stimulation of growth was sufficiently great that these insects were not able to suppress it for a 2-6 week period. Eventually all of the new branches had their shoot tips eaten and no further stimulation took place. The new growth was of a type not normally encountered on insolated shoots. The branches had long internodes and thin thorns; there were 3-15 such branches per shoot. In treatment subplot S-1, the stimulation caused an increase in mean height of 21.5 cm (difference between the growth in the treatment and control subplot). It was in S-1 that the greatest stimulation took place. No attempt has been made to extract this height increase from the mean values obtained for any of the treatment subplots.

Clipping thorns. In December 1963, it was realized that the distal portions of a swollen thorn are dead tissue and therefore can be removed without damaging the shoot or stimulating it (Fig. 41a). There is ample evidence from natural damage that removal of the distal ½-¾ of a green but stiff thorn does not affect its leaf. When clipping thorns with pruning shears, care must be taken not to rupture the junction between the thorn and the bark. Preliminary trials showed that if all the thorns on a shoot are clipped off about the one-half way between the point and the base, almost the entire colony is destroyed or lost through disorganization. On these shoots, the surviving workers and brood concentrated themselves in the thorns produced during the next 2-4 weeks and could be clipped off. Searching queens do not establish colonies in the clipped thorns. There is no leaf drop or color change on these shoots, and no stimulation of growth in dormant shoots. These shoots are not acceptable as auxiliary-shoots until they have grown new thorns. In order to avoid this problem, the acacia plants were removed whenever possible around the new subplots for a distance of 2-3 m.

In four different cases, raiding columns of *Nomamyrmex esenbecki* went through the subplots within a week after clipping and were partly responsible for removal of the ants. In two cases, swarm raids of *Labidus praedator* did the same thing. When a thorn was clipped, the brood was scattered on the ground, and *Solenopsis geminata* and other ants were generally responsible for its loss. Rain drowned the workers and brood in the opened thorns.

While clipping thorns was time consuming, it was also very effective. A number of subplots with clipped thorns were completely free of workers by June 1964.

Recolonization of treated plots. Ideally, the treatment subplots should contain only unoccupied shoots and the control subplots only occupied shoots. In actuality, at the last recording only treatment subplots C-1, E-2, H-1, K-1, L-1, M-1, N-1, O-1, and Q-1 contained no occupied shoots; thorn clipping had been used in all of these. The other treatment subplots had various numbers of occupied shoots in them due to invasion from colonies outside the subplot, or due to young colonies developed in situ. In the control plots, the percentage of occupied shoots ranged from 80-98 percent at the last recordings made between 26 Jul. and 8 Aug. 1964.

Most of the subplots were mapped and individual shoot records kept for most of the subplots' histories. This means that in addition to the possible comparisons between subplots, the occupied shoots in the plot can be contrasted with the unoccupied shoots in the plot.

Invasion from outside of the treatment subplot can be prevented by removing the shoots of *A. cornigera* for a distance of 5-10 m around the subplot. This cannot be done to control subplots because of the likelihood of removing the queen-shoot that is associated with auxiliary-

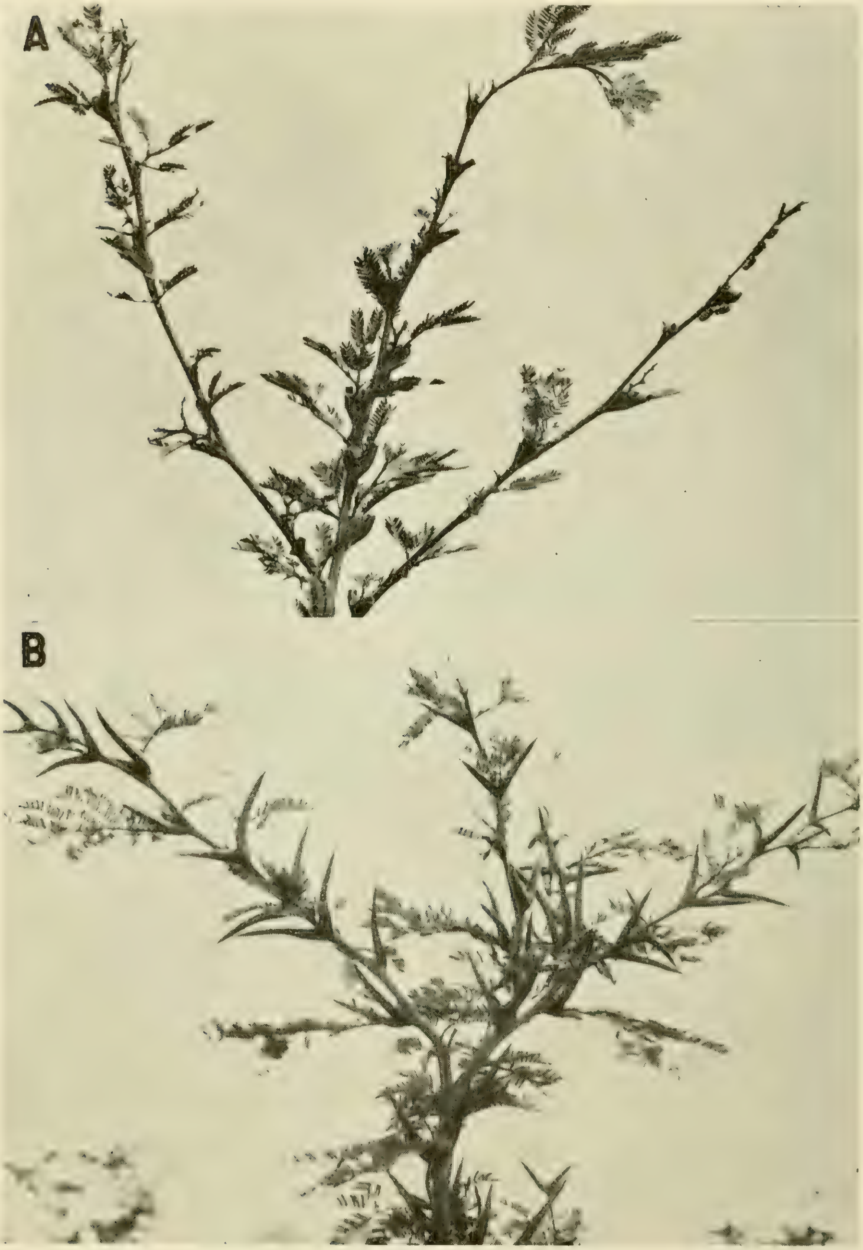


FIG. 41. a. The canopy of a shoot of *Acacia cornigera* in treatment subplot N-1. The thorns were clipped on 3 Apr. 1964. Five males of *Anomoea* sp., probably *A. rufifrons,* can be seen near the end of the right-hand branch. This shoot would be rated as a number 2.5. Photo 25 Jul. 1964. b. The canopy of a shoot of *Acacia cornigera* in treatment subplot S-1. The shoot has not been occupied since late in 1963. This shoot would be rated as a number 2.5. Photo late July 1964.

shoots within the subplot. The fact that treatment subplots E-2, H-1, L-1, M-1, and Q-1 were free of workers at the last recording is due to this type of shoot removal. In treatment subplot N-1 and O-1, in order to insure that the shoots with clipped thorns stayed free of workers, all shoots less than 50 cm tall were removed. This removed the founding queens and small colonies living in these suppressed shoots.

Removal of vegetation adjacent to *A. cornigera.* The amount of surrounding vegetation adjacent to the shoot may influence the amount of phytophagous insect damage or cattle grazing on *A. cornigera.* Several subplots were established in which all vegetation besides *A. cornigera* was cut to ground and the shoots of *A. cornigera* that were less than 100 cm tall were removed. The cut vegetation was not burned, but it is doubtful that it had a substantial effect as a fertilizer during the experiments. This technique approximates normal conditions since in vegetation that is being cleared by hand for pasture, the shoots of *A. cornigera* that are over 3 m tall are sometimes not cut because of the shower of ants which falls when the trunk is hit with a machete.

Clearing of all vegetation. Several subplots were established by cutting all the vegetation to ground level but not burning the litter. Where this vegetation was over 1 year old, the stumps of *A. cornigera* were cut at 65 cm to facilitate finding them in the future regeneration. Since the new suckers often started at some point above the base on the trunk, the lengths of the shoots as well as their heights were recorded.

When all the vegetation is cleared and the shoots of *A. cornigera* contain large colonies, a third type of treatment subplot is made. In the treatment subplot, the canopies of the *A. cornigera* shoots are piled and burned. Any colonies that are to occupy the suckers from these unoccupied stumps must develop in situ, or move in from outside the subplot. In the control subplot, the canopy is placed across its cut stump. The workers patrol the stump and as the new suckers appear (within 3-10 days) they are immediately occupied by the colony. Auxiliary-units transfer into the new suckers in the same manner as do queen-units. However, if the stump is very slow to produce new suckers, the auxiliary-unit may retract into the queen-unit or move to a different stump.

Enclosure in barbed wire. Subplots enclosed in barbed wire were intended as contrasts to subplots to which cattle had access. Three strands of wire were used. The enclosures were in general too small (6 by 6 m or 6 by 12 m) since cattle could, and did reach in at least 1 m to browse. Final recordings were not made in these plots since the cattle were removed from the control subplots by their owner before the rainy season began.

Adding units. A mature colony may be added to an unoccupied shoot by cutting an isolated queen-shoot with a large worker force and placing it in contact with the shoot. Cutting an auxiliary-shoot and placing it on the unoccupied shoot will provide occupation for 1-2 months but eventually the worker force is lost.

Multiple treatment. In several cases, it was necessary or of interest to use more than one of the above treatments on a subplot. The effect of the presence or absence of a worker force is of central interest in this study, rather than the effect of the treatment on the shoot. Because of this, any treatment, or set of treatments that would insure the removal of the worker force without damaging the shoot or phytophagous insect population was used.

Recording data. Shoot identification. The individual subplots were the original experimental unit. However, it soon became evident that some method of individual shoot recognition was necessary. This was because of the lack of subplot replicates, the variation in shoot height among even-aged shoots within a subplot, the presence of occupied shoots in treatment subplots, and the unoccupied shoots in control subplots. Placing individual numbers on the trunks was too slow and tags were stolen. Mapping the location of the shoots proved very successful. It simplified the location of the shoots and insured that all the shoots were counted in each recording. The majority of the subplots were mapped by January or February. The consequence of mapping is that each subplot can be treated as a set of *n* replicates. In later analyses each shoot can be regarded as an independent unit which is or is not occupied. Due to the presence of auxiliary-units, all occupied shoots were actually not independent of each other, but time was not available to determine which shoot had which kind of units.

Height. The height of the shoot is the distance above the ground of the highest node. This was measured to the nearest cm in subplots with most of the shoots less than 2 m tall and to the nearest 5 cm in subplots with most of the shoots over 2 m tall. When regeneration from experimentally cut stumps was measured, the length of the tallest shoot from the stump was recorded as well as the shoot height. When it was obvious that two or more major shoots had grown from a single stump, only the tallest was recorded. Such paired shoots are always occupied by the same colony.

Height of surrounding vegetation. Because of the detrimental effect that shading has on *A. cornigera,* the height of the immediately surrounding vegetation was often recorded in ungrazed or in lightly grazed subplots. In heavily grazed subplots, there was essentially no shading of any shoots. When the height of the individual shoot was measured, the height of the nearest other species of plant that was not damaged by *P. ferruginea* was recorded. The mean of these measurements serves as an indicator of general canopy height in the subplot. When this mean is subtracted from the mean height of the shoots of *A. cornigera,* the amount of emergence of *A. cornigera* can be obtained.

Condition of the shoot. Since the degree of damage to the uppermost growing points or highest nodes is a measure of potential height increment within a plot, the condition of these points was recorded. The following numerical scheme was used, grading from a perfect terminal to a dead shoot.

(4) The point to which the height is measured in an undamaged shoot tip, and the mature foliage shows little or no animal or fungal damage. Fig. 42, 43, 44.

(3.5) There are two main shoots of subequal height from the same stump, one of which is a #3 and the other a #4.

(3) The shoot tip at the uppermost node has been destroyed and any new shoot tip on the shoot has not yet attained this height. These shoots have little or no damage to their mature leaves and have growing points lower down on the shoot. Fig. 42, 43, 45, 46.

(2.5) Both the uppermost growing point and lateral growing points are destroyed, and the mature foliage shows 25-50 percent removal. Fig. 40, 41, 47.

(2) The shoot is like #2.5, but 50-75 percent of the mature foliage has been removed.

(1.5) The shoot looks dead but still has a green layer under the bark and perhaps one or two leaves. Fig. 48.

(1) The shoot is dead but still standing.

(0) The shoot is gone or at least has fallen over. Normal leaf drop is not regarded as damage. While it would be difficult for an untrained observer using this scheme to arrive at the same subplot numerical evaluation of condition as would the author, it is felt that evaluation has been consistent throughout the study. All subplot evaluation was done by the author.

Causal agent of condition. The specific feeding damage of *Coxina hadenoides,* leaf rollers, webbing larvae, *Syssphinx mexicana, Mozena tomentosa, Pelidnota punctulata, Onicideres poecila, Lochmaeocles cornuticeps,* Chrysomelidae, cattle, rodents, and birds can be recognized and at times during the spring of 1964 was recorded individually. The damage of *Coxina hadenoides,* kathydids (Tettigoniidae), and some Chrysomelidae is easily confused and therefore was recorded as one.

Presence of foreign objects. The presence of vines and animals on the shoots was usually recorded. They were not collected within the subplot since a single organism can have a great effect on growth.

Presence of *P. ferruginea.* To obtain maximum assurance that shoots recorded as unoccupied did not have workers in the thorns, the subplots were recorded only on days when the maximum temperature was over 29° C. If possible, records were made when the temperature was over 32° C. The presence or absence of workers was recorded, or else the actual number on the shoot counted and recorded. During the counting process, the shoot was not disturbed. The presence of entrance holes in the thorns does not insure that there is a worker force present in the shoot. The entrances in new green thorns may be made by founding queens. The presence of many terminal thorns without entrances usually indicates the lack of a worker force. Since Beltian bodies were commonly removed by *Pseudomyrmex gracilis mexicana* and *Solenopsis geminata,* the absence of these structures does not insure that there is a worker force present. The larger entrance holes of *P. gracilis mexicana* can often be located by inspection and if there are more than 2-3 workers of this ant seen on the shoot surface, there is not likely to be a worker force of *P. ferruginea* in the thorns.

Ideal plot. Because of mistakes made in plot establishment, it seems advisable to clarify what plan should be followed to establish plots of maximum usefulness. Some of the most informative rectangular plots established in this study were those in which all of the vegetation was cleared to ground level, the canopies of *A. cornigera* were piled and burned in the treatment subplot, and the canopies were left next to the stump in the control subplot so that the colony could invade the new suckers (e.g., plots A, E, H). This was done in plots that had been regenerating for more than a year. To obtain the maximum amount of information this plot should be split into at least three subplots. One subplot is the control, one has the canopies removed, and one has the thorns of the new growth clipped as well as the canopies removed. The ideal plot should be replicated during the period of the experiment. The subplots should be at least 20 m apart and have at least 100 stumps in each. The subplots should be cut out of a relatively uniform stand of vegetation, must be mapped, and must have all the *A. cornigera* removed to a distance of 10 m around each treatment subplot. This cannot be done around the control subplot due to the danger of removing a queen-unit of one of the auxiliary-units in the

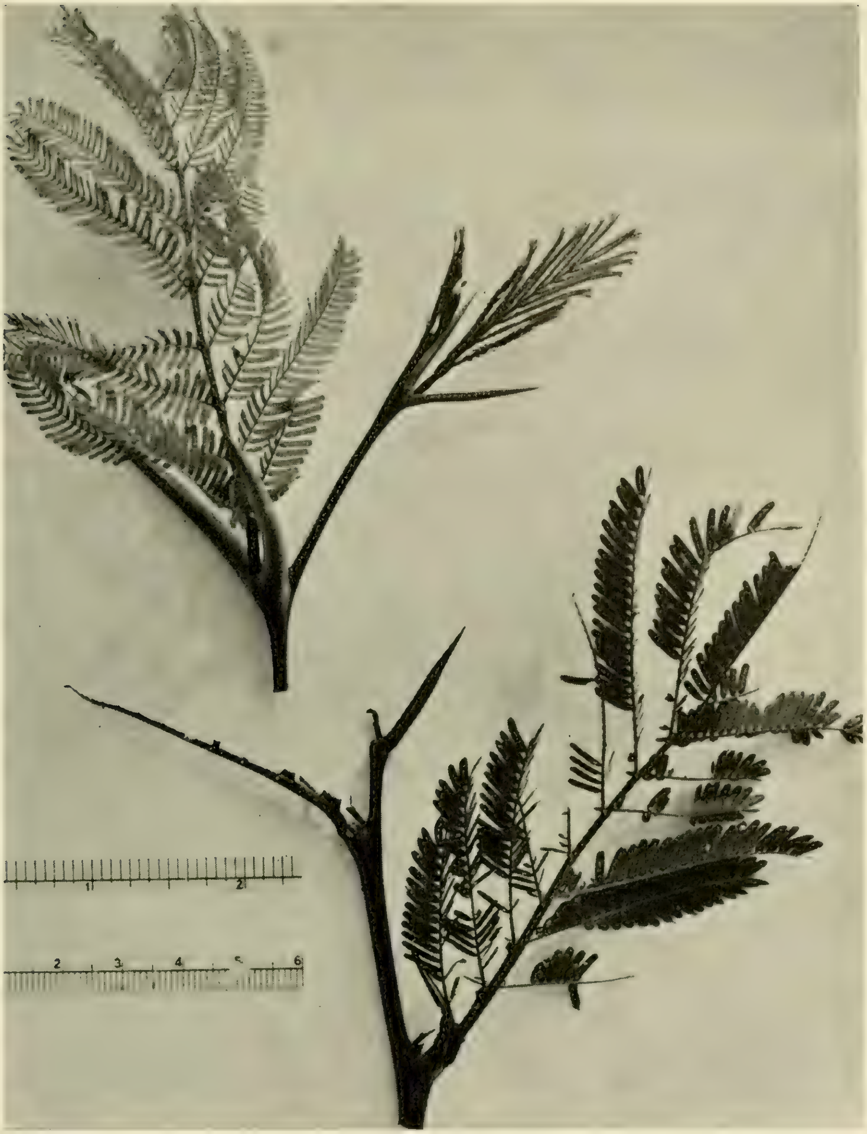


FIG. 42. The upper left-hand shoot tip of *Acacia cornigera* is undamaged and would be rated as a number 4. The lower right-hand shoot tip was damaged by *Coxina hadenoides* and would be rated as a number 3. Photo late July in plot P.

subplot. The stump diameter should be recorded as an index to the size of the parent root stock. It is best not to set up such a plot during the cool season because transfer of the colonies in the control subplot is slowed at this time.

At least once every two months, the heights and lengths of the sucker shoots, the height of the surrounding vegetation, the condition of the shoots, and the presence of other organisms on the shoots should be recorded. The newly produced thorns in the second treatment subplot

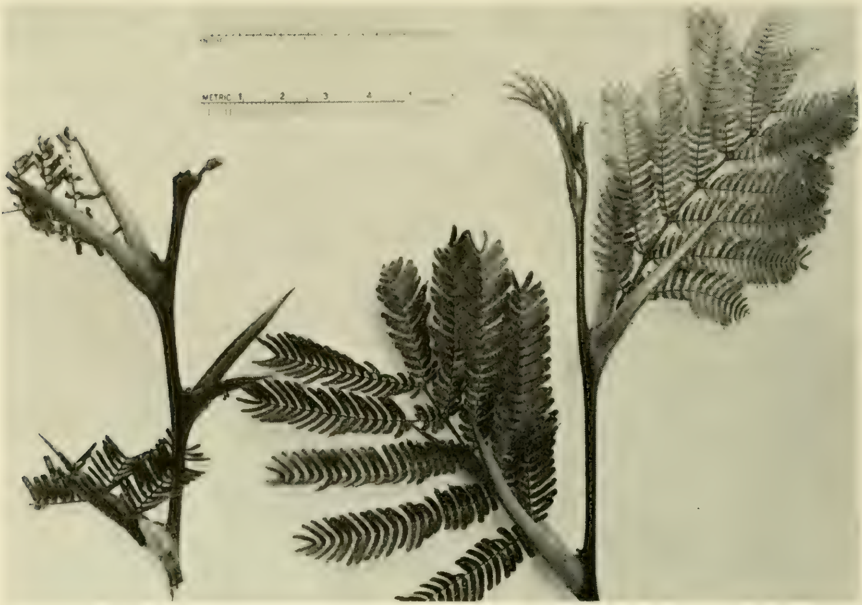


FIG. 43. The left-hand shoot tip of *Acacia cornigera* was damaged by *Pelidnota punctulata* and would be rated as a number 3. The right-hand shoot tip is undamaged and would be rated as a number 4. Photo late July in plot M.

should be clipped about every four months. About every two months, and at each major change in the weather, a nocutrnal and diurnal recording of the presence of phytophagous insects on the shoots should be made. Specimens can be collected from one of the replicates for identification. From this same replicate, samples of entire colonies can be made to determine colony growth rates and sizes in the first treatment subplot. If possible, cattle should be allowed to graze heavily in one of the replicates and be excluded from another. The more frequently and closely the shoots are examined for phytophagous animals and their damage, the more information will be obtained. Some insects are present only during very specific times of the day, and for a very few days.

After about 1½ days of such a schedule, nearly the maximum amount of information available, as to the effect of *P. ferruginea* on *A. cornigera,* will have been obtained. In the first treatment subplot, those shoots that survived long enough to produce colonies will be growing at the same rate as those in the control subplot. The shoots in the second treatment subplot will probably all be dead.

In natural disturbance sites such as arroyos and river banks, the shoots of *A. cornigera* are often highly dispersed. In these cases, linear plots yield the most information (e.g., plot B). Such a plot consists of a long row of unevenly spaced shoots, some of which are treated and some of which serve as controls. The treatment, mapping and recording of data should be as in the rectangular plot discussed above. Such a linear plot may be several kms or more in length, and pass through a large number of microhabitats. It seems preferable to alternate the treatments from stump to stump rather than from one section to another of the plot. Therefore it is as if the three subplots are superimposed. Rather than use a strictly random method to determine what treatment an individual stump will receive, an attempt, where possible, should be made to have an even alternation between controls and treatments throughout the length of the plot.

In linear plots, the decision as to what shoots can be used for controls, and what shoots can be used for treatments is influenced by the presence of auxiliary-shoots. No treatment shoot should be within 15 m of a control shoot, or a shoot not included within the plot (these latter shoots can be completely removed). When the canopy of the treatment shoot is removed, it should be totally destroyed or moved to a distance at least 20 m from any other treatment shoot. The shoots within a cluster of shoots (e.g., 4 auxiliary-shoots and 1 queen-shoot), because of

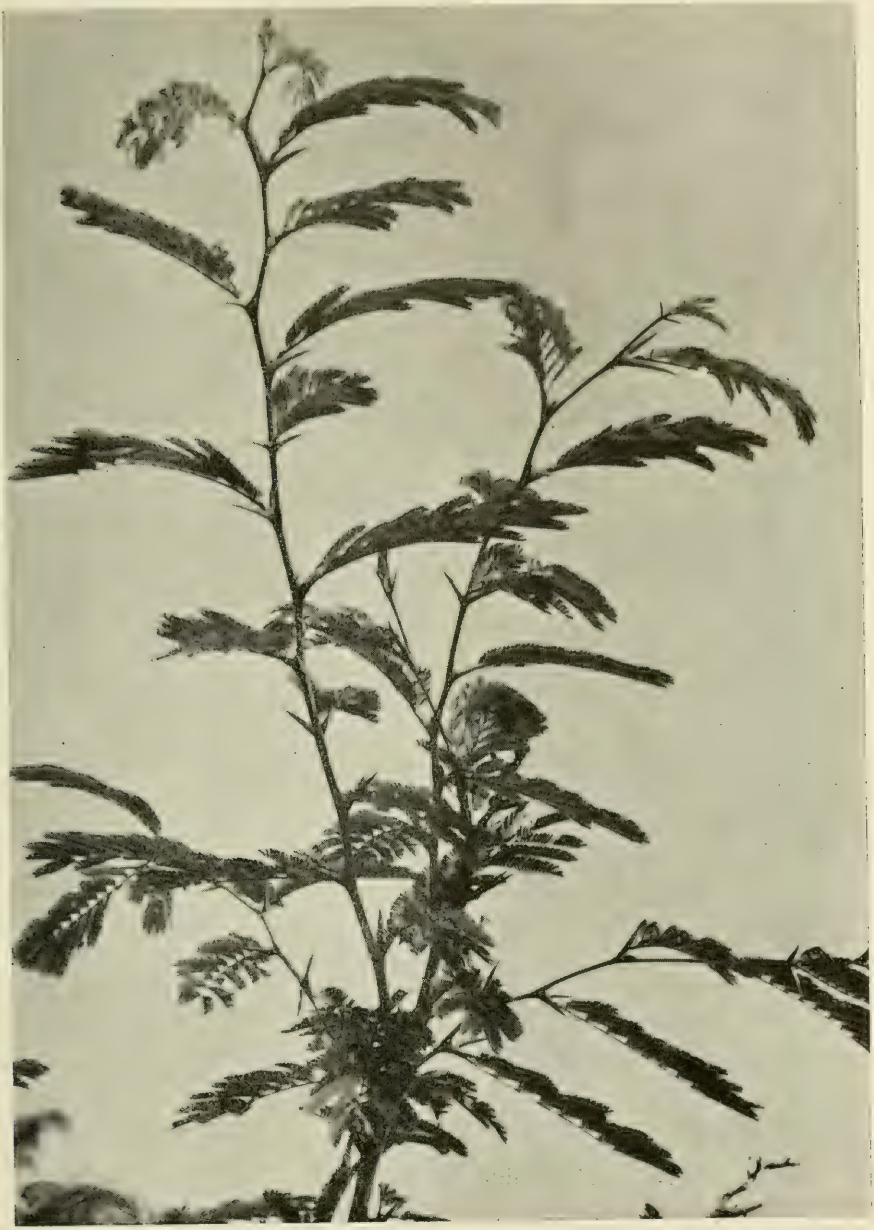


FIG. 44. The canopy of an occupied shoot of *A. cornigera* in control subplot N-2. This shoot would be rated as a number 4. Photo late July 1964.

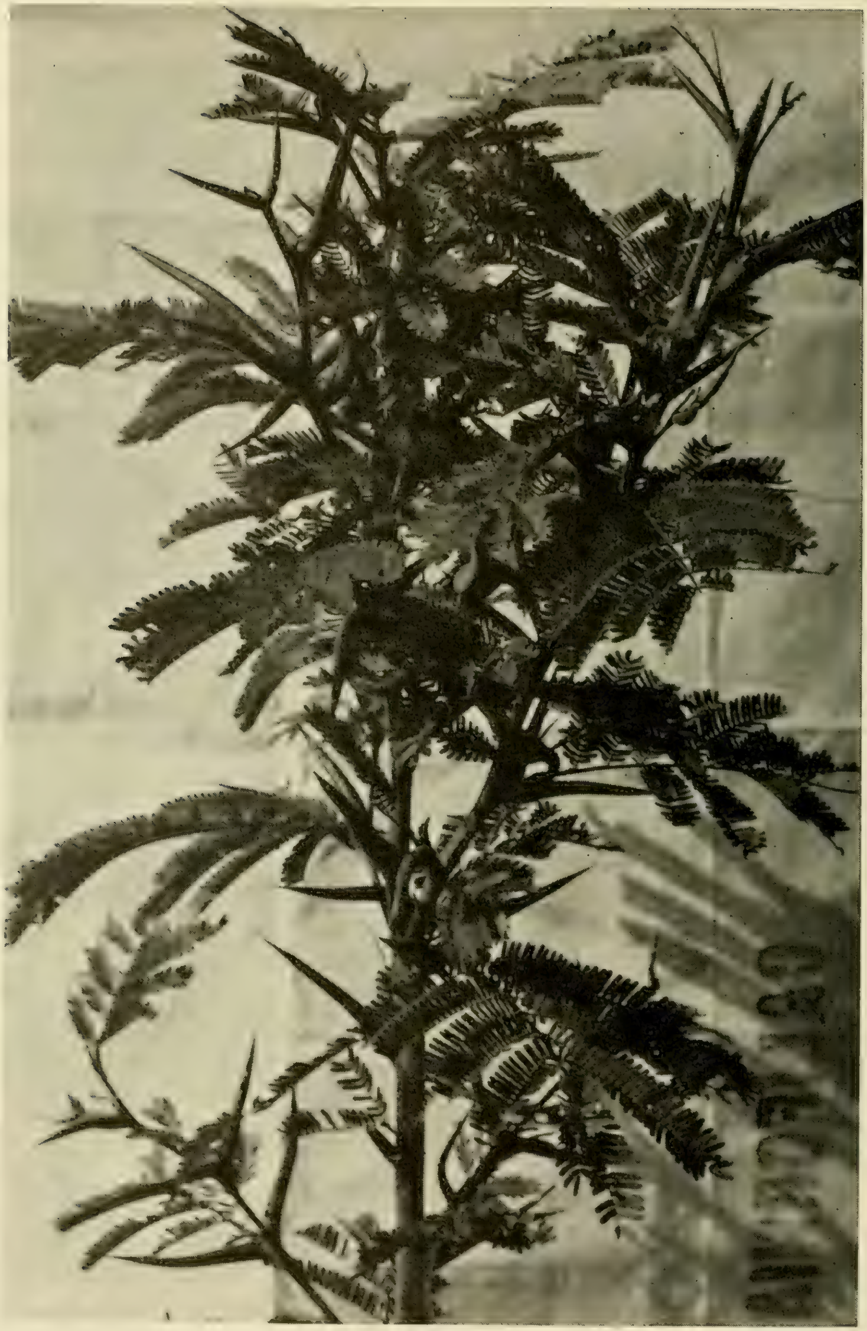


FIG. 45. The canopy of an unoccupied shoot of *A. cornigera* in treatment subplot N-1. This shoot would be rated as a number 3. Note that there are at least four number 3 shoot tips in the top of the canopy. This damage was caused by *Coxina hadenoides* and adult tettigoniid grasshoppers. The ants were removed by parathion on 12 Oct. 1963. The shoot was a number 4 at that time. Photo 28 Nov. 1963.

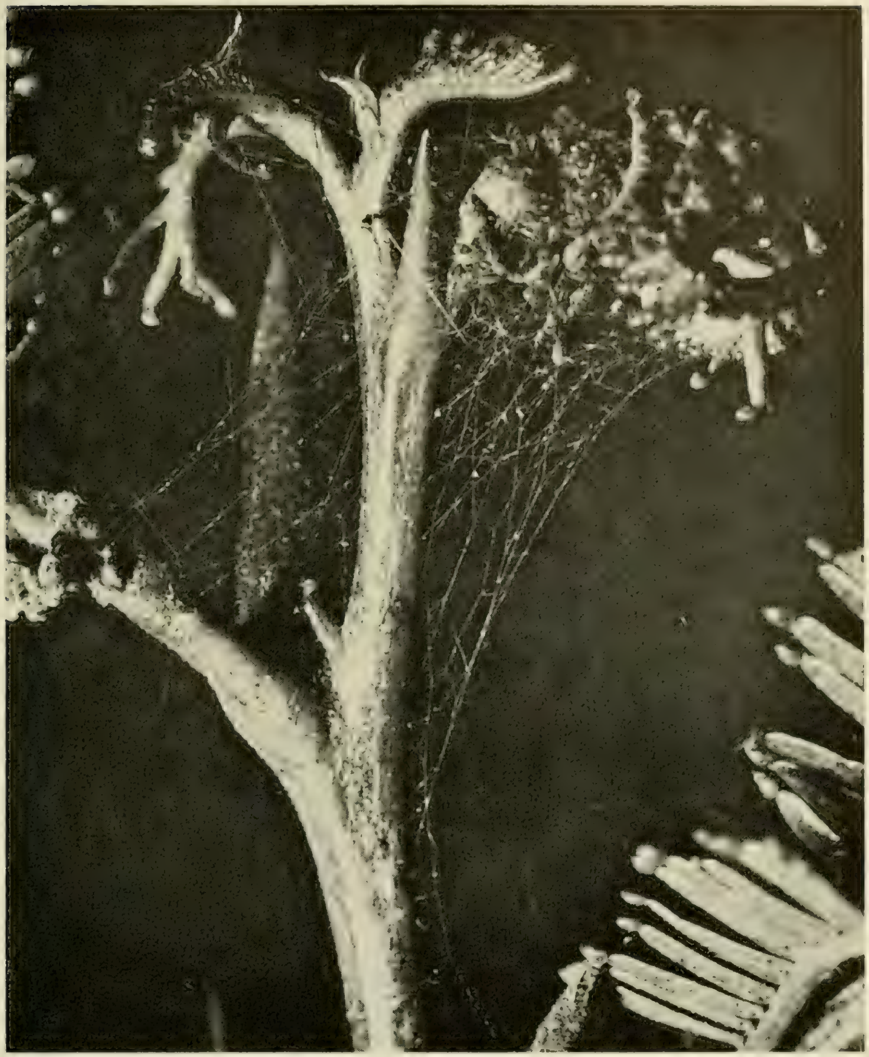


FIG. 46. A shoot tip of *Acacia cornigera* during the cool season. The shoot's colony of *P. ferruginea* was removed with parathion in late 1963. This shoot tip was a number 4 until a black sooty mold began to grow on the sticky material that covers the shoot tip. This mold killed the shoot tip. It is now a number 3. The webbing is that of a spider from the right-hand curled and stunted leaf. Photo 23 Dec. 1963 in treatment subplot N-1.

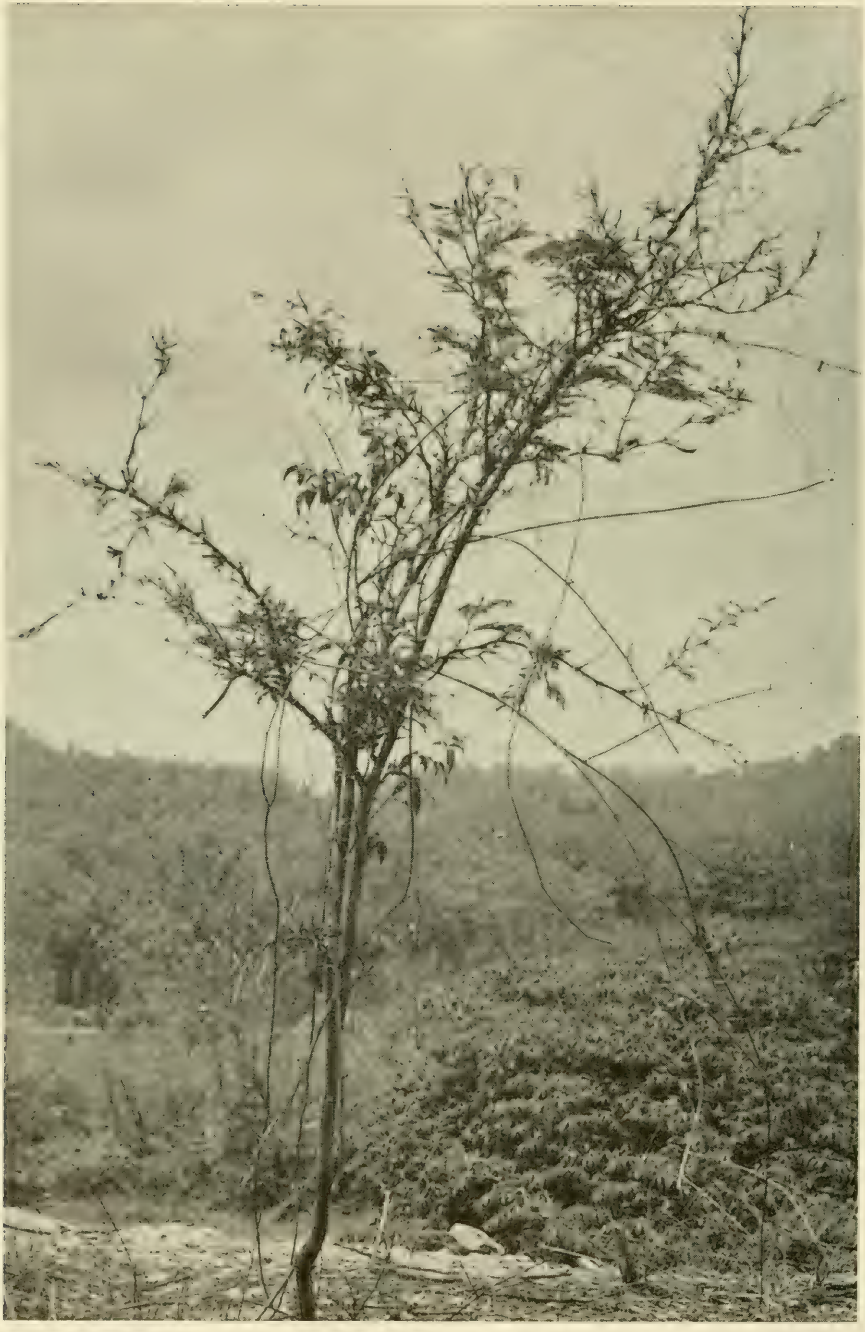


FIG. 47. A naturally unoccupied shoot of *Acacia cornigera* growing in plot B. This shoot was apparently never occupied by *P. ferruginea.* It was occupied by a large colony of *Crematogaster* sp. at the time the photograph was taken. Note the dead vines in the canopy and the lack of mature leaves. This shoot would have been rated a number 2.5. Photograph taken in late July 1964.

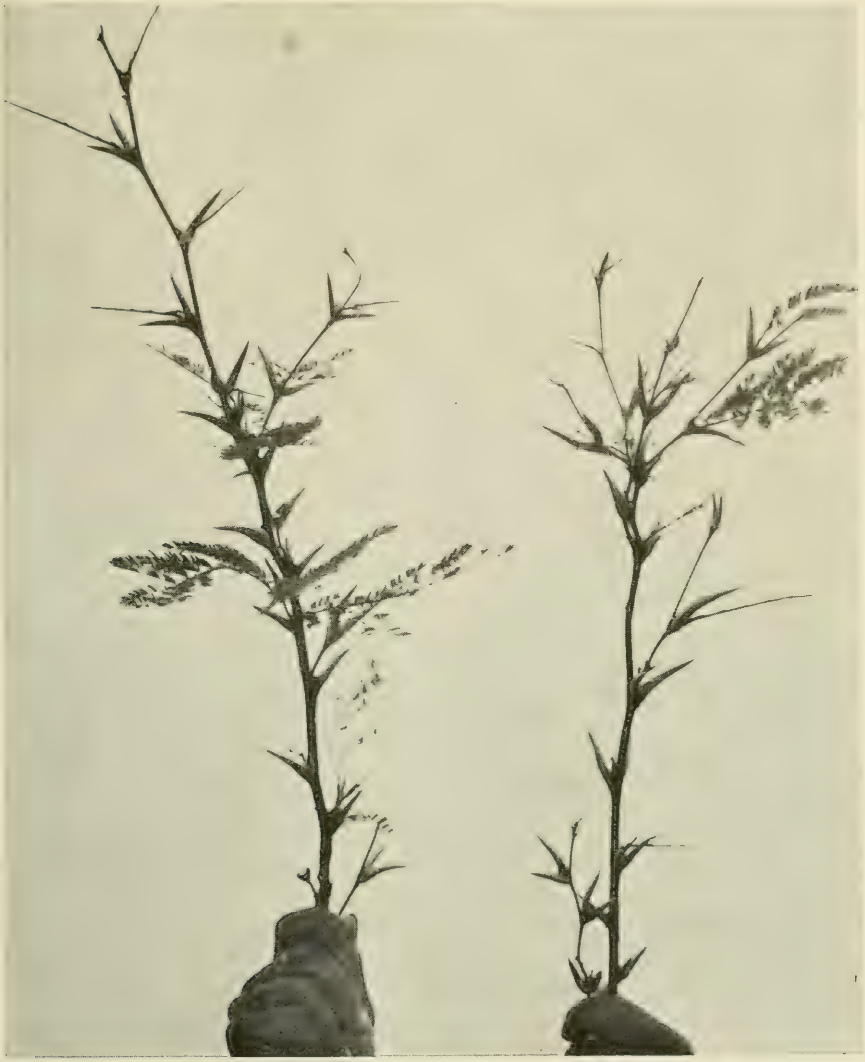


FIG. 48. Two naturally unoccupied shoots of *Acacia cornigera.* They were rated as number 1.5. They were growing in treatment subplot S-1 and are of the size often eaten by *Sigmodon hispidus* during the dry season. Photo late July 1964.

their proximity to each other, must all be controls or all be treated. However, each shoot can be counted as a single shoot. The occupant ant colony must be identified (*P. ferruginea* or *P. nigrocincta* in the Temascal area).

A linear plot of this type should include as many plants as time permits because 5-20 percent of the shoots are invariably destroyed by someone using the cut canopies from the controls for fencing, or invasion of the treatment shoots by an unnoticed colony, or a colony from an undestroyed but removed canopy.

Statistical treatment of data. The statistical tests in this study involved the contrasts of two population means $(\bar{X})$ for which a sample standard deviation (s.d.) or variance (s^2) was calculated. In this case, the null hypothesis was that the mean of the first population (U_a) was equal to the mean of the second population (U_b), or $H_o: U_a = U_b$. If accepted, this hypothesis would indicate that *P. ferruginea* has no effect on *A. cornigera.* The sample means used were those of the control subplot or the group of occupied shoots ($\bar{X}_a$), and those of the treatment subplot or the group of unoccupied shoots ($\bar{X}_b$). $\bar{X}_a$ was chosen to represent the occupied shoots since it was expected that these means would be larger.

The statistics used was $Z = \frac{(\bar{X}_a - \bar{X}_b)}{\sqrt{\frac{s_a^2}{n_a} - \frac{s_b^2}{n_b}}}$ with the value for rejection of the null hypothesis being Z greater than 1.645 (significant difference between the means $p < 0.05$) and Z greater than 2.326 (highly significant difference between the means $p < 0.01$).

The use of the Z test of significance between the two means required that the variables (individual height or length increment, and condition) be independent observations. This was assumed for this study, although in reality the presence of the auxiliary-shoot effect means that the height or length increment, and the condition value, of an individual shoot is to some degree correlated with the number of ants on neighboring shoots. Queen-shoots usually have larger colonies and consequently show large increments in height or length; large queen-units usually have large auxiliary-units, which also have large increments in height or length.

The use of the Z test of significance did not require that the variables be distributed normally. However, most of the sets of variables recorded as height or length increment, and condition, were not too badly skewed. This was especially true when groups of continuously occupied shoots were compared with groups of continuously unoccupied shoots.

The Z test of significance is usually used when the variances of the two populations are known (they need not be equal). For the purposes of this study, it was assumed that the sample variances obtained approximated the actual population variance. It is generally considered that this assumption is justified when the sample size is over 30 (Nissen-Meyer, personal communication). In most of the comparisons in this study, this was the case. However, the Z test was also used when the sample size was less than 30 for two reasons. One reason was for consistency. The other was that, on the basis of many observations made inside and outside of the experimental plots, it was felt that the variances recorded for most of the smaller sample sizes would not have been greatly changed had the samples been larger.

Negative Z values were occasionally obtained in both the contrasts of height increment and condition. Occasionally, these values were low enough to be significant. The reasons for these significant negative Z values are the same as those for the low Z values that were not significant. The major reason was the presence of occupied shoots in the treatment subplots, and occasional unoccupied shoots in the control subplots. Of secondary importance was the production of short vegetative or flowering branches following the stimulation of growth by parathion or insect damage. These secondary effects were of only temporary importance and disappeared before the 1964 rainy season began. The primary reason for significant negative Z values can hardly be used as evidence against a positive effect of the ants on the acacia; it must be regarded as a product of faulty experimental design.

It should be noted that of the $\bar{X}_0$ and $\bar{X}_{inc}$ columns in Table 4 through 13, the $\bar{X}_{inc}$ values are those used in the tests of significance. The $\bar{X}_0$ column contains the mean heights at the beginning of the interval over which the increment occurred.

PLOT DESCRIPTIONS

The following plot and subplot descriptions are presented as documentary materials, and to enable comparisons of the experiments in this study with similar experiments in other studies. The descriptions are arranged beginning at Temascal and progressing to the east. At each general area they are arranged by the age of the occupied shoots of *A. cornigera* at the time of the first treatment. During the course of the experiments, 70 subplots were established and 20 of these were destroyed by burning, dynamiting, clearing, or changes in management plans by the owner. Those remaining are plotted in figure 7. The descriptions of some subplots are included even though they were destroyed since they aid in comparisons between other subplots. All cattle were removed by the owner from plots C, E-I, K, N-Q, and S-V, after 3 May so that the barbed wire cattle exclosures near these plots were rendered useless in respect to examining the effect of cattle on *A. cornigera.* The descriptions of these exclosures are omitted.

The following data are presented for each plot: exact locality, photograph if available, purpose of plot and subplots, history and size, vegetation physiognomy, plant species composition, representativeness of the plot, characteristics of *A. cornigera* and *P. ferruginea* before treatment, kind of treatment, characteristics of *A. cornigera* and *P. ferruginea* after treatment, animals present in the plot, and comments.

B

Plot B was a linear plot extending 2.5 km south from the north end of the Presa Miguel Aleman along its eastern base (Fig. 49). It was 2.5 km northwest of Temascal. The treatment subplot (B-1) was superimposed on the control subplot (B-2) because the treated shoots alternated with control shoots.

Plot B was established later than most plots (24 Apr.). It was intended as a plot of sucker regeneration in which the individual treated shoots would be free from reinvasion. The site was chosen because the open plant community insured that all shoots of *A. cornigera* would be found, and because of the presence of widely spaced 2-5 year old shoots with large colonies. When the shoots were cut, the canopies of the stumps that were to be ant-free were carried at least 15 meters from their stumps. They should have been burned. The lack of living shoots in the areas where the canopies were thrown caused the workers to wander very long distances in search of *A. cornigera*. By 6 Aug., 19 of the 53 units removed from the treated stumps had found their way back to the stump.

The site of plot B was freshly quarried limestone and sand in 1958. Examinations of annual rings of the shoots of *A. cornigera* indicated that all the acacias on the site were seedlings and the oldest germinated in 1959. The site had never been cleared except for random cutting of fence poles. It was grazed by cattle and goats since 1958. The area from which treated and control shoots were chosen was about 7 acres in size.

In general appearance, the vegetation formed an open plant community. Patches of trees and shrubs 2-5 m in height and 8-15 m in diameter were scattered over relatively bare ground with sparse grasses and broadleafed herbs. There were few woody vines in the patches of trees but during the rainy season herbaceous vines covered large areas. Plot B was margined on the west by piled bare limestone and on the east by dense second growth forest with a canopy 5-15 m high.

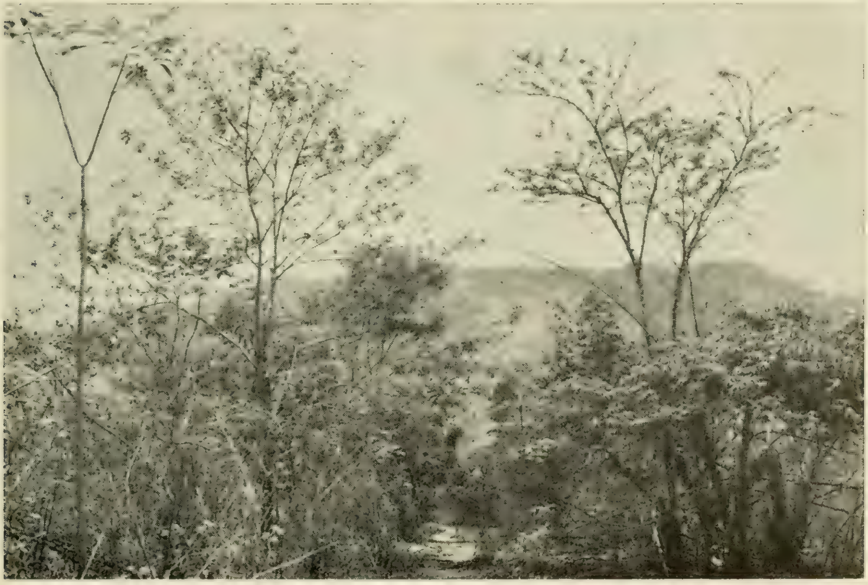


FIG. 49. Looking north through plot B. The shoots were cut along both sides of the trail in the center of the photograph. The tree on the far left with a single upper branch fork is *Tabebuia pentaphylla*, the large tree to the right of it is *Ateleia pterocarpa*, and the tall tree on the right-hand side of the trail is *Acacia cornigera*. The low tree below it is *Muntingia calabura*. The *A. cornigera* is about 9 m tall and occupied by a colony of *P. ferruginea* with about 15,000 workers in it. Shoots of this type were cut to obtain the sucker regeneration in plot B. Photo April 1964.

The plants growing in plot B were characteristic of natural and man-made disturbance sites in the Temascal area. The trees were *Muntingia calabura* (3-5 m), *Cecropia obtusifolia* (5-10 m), *Ateleia pterocarpa* (5-7 m), *Pterocarpus* sp. (5-7 m), *Acacia cornigera* (3-8 m) and *Acacia chiapensis* (3-5 m). The shrubs were seedlings of the above species of trees plus *Calliandra houstoniana, Conostegia jalapensis, Bauhinia ungulata,* woody Compositae, and Leguminosae.

Before any shoots were cut in plot B, there were four shoots with the thorns inhabited by a colony of *Crematogaster* sp. and/or *Pseudomyrmex gracilis mexicana*; these shoots were not included in the plot as they were nearly dead. Five shoots were occupied by large colonies of *Pseudomyrmex nigrocincta*; these were treated as if they were colonies of *P. ferruginea,* even though they were not quite as effective as was *P. ferruginea* in patrolling the shoot. The colonies of *P. ferruginea* in the plot were large and all over two years old. The shoots of *A. cornigera* were sufficiently scattered so that about one-half of the shoots had queen-units in them. Most of the shoots of *A. cornigera* bore flowers or fruit. In many cases, the shoots were emergent through the thin canopy of *Muntingia calabura* and the shade was sufficient to cause the sucker shoots from the cut stump to take on a slightly attenuated life-form.

The shoots of *A. cornigera* were cut at 65 cm and the canopies of 53 removed and the canopies of 47 left across their stumps. All of the 100 stumps initiated regenerating suckers. During the following weeks of observation there were some occupied suckers in the treatment subplot owing to reinvasion by the ants and some unoccupied suckers in the control subplot owing to the death of one colony and the loss of several canopies to persons seeking fencing material.

During the period of the experiment, cattle and goats grazed and browsed the area on a daily basis. Except for the various species of *Diplotaxis,* the insects usually found feeding on occupied and unoccupied *A. cornigera* were all observed in plot B. *Coxina hadenoides* was especially abundant and an unoccupied shoot rarely passed more than one night without having the shoot tips eaten. *Sigmodon hispidus* damage was observed in this plot.

There was almost no seedling reproduction of *A. cornigera* in plot B. Occasional seedlings were found under *Muntingia calabura* where they had been dropped by birds eating the fruits of *M. calabura.* On one occasion in plot B a black squirrel was observed eating the undamaged shoot tips of an unoccupied 2 m tall shoot.

KA, K, N, O, P

These five plots were established in young regeneration in the brushy pasture 30-200 m north of the Temascal-La Granja highway and 5-200 m west of El Mocho's house on the land of Señor Eusavio Farfan. El Mocho's house is 5 km east of Temascal. Within each plot, rectangular treatment and control subplots were established.

It was originally anticipated that these five plots would be lightly grazed throughout the experiment; however, the cattle were removed by 3 May 1964 and therefore the major portion of the growth took place in the absence of cattle. Plots KA and K were intended for examination of the growth from vegetation cleared to ground level but not burned; unfortunately it was not practical to map them with the amount of time available. Plots N and O were intended as a contrast to plot P; in the former plot, the surrounding vegeation was cleared but at first all shoots of *A. cornigera* were not cut (Fig. 50) and later only those that were occupied (taller than 50 cm) were not cut. In plot P no vegetation was cut.

The regeneration in these five plots was part of a cycle of cutting and browsing and occasional burning to produce more browse. It was last cut to the ground in January 1963 but it was not burned at that time. The previous vegetation was cut in August 1962 and again not burned. No cattle were present from June 1963 to 3 Dec. 1963; they were then removed on 3 May 1964. The land was cleared of forest in 1940. It had been occasionally used for corn fields before 1956. The areas in square meters of the various subplots were as follows: KA-1, 107; KA-2, 90; KA-3, 108; K-1, 102; K-2, 108; N-1, 258; N-2, 212; O-1, 197; O-2, 183; P-1, 445; and P-2, 222.

In general appearance, the area containing the five plots was a dense stand of herbs, shrubs and tree suckers from old rootstocks in September 1963. The canopy was about 75 cm above the ground and densely interlaced with herbaceous and woody vines. Projecting through this rather even canopy were scattered 1-2 m tall occupied shoots of *A. cornigera.* Below the canopy were much more numerous heavily shaded and unoccupied shoots of *A. cornigera.* During the experimental period, the vegetation that had been cut in plots KA, K, N and O regenerated a plant community with the same life form. During the period that cattle were present, nearly all herbaceous vines were eaten and the shrubs were lightly browsed. Along with the leaf drop during the dry season, this activity opened the canopy, but it filled again when the rains started and the cattle were absent. By August 1964, the general canopy in plot P was about 180 cm

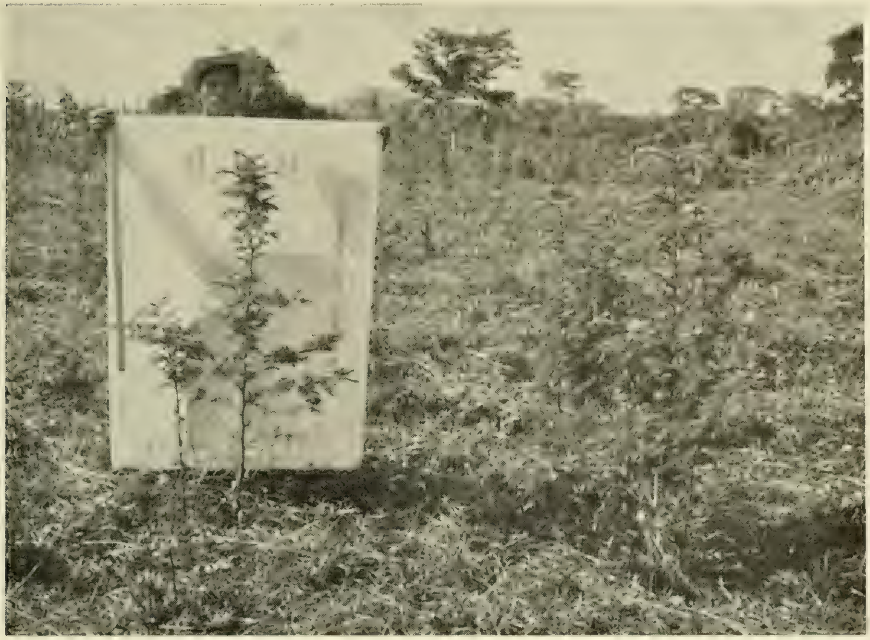


FIG. 50. General aspect of treatment subplot N-1 immediately after the general vegetation was cleared in October 1963. The plant in front of the sheet is *Acacia cornigera* and is occupied by a colony of *P. ferruginea* with about 1,500 workers in it. The smaller shoot to the left is an auxiliary-shoot to the taller queen-shoot. The cluster of shoots in the right-hand side of the photograph is a queen-shoot with four auxiliary-shoots.

tall and the heavily occupied shoots of *A. cornigera* were still emergent by 25-150 cm. There were a few old trees 4-8 m tall in the five plots but they did not provide continual shade for any portion of the plots.

The outstanding trees were *Tabebuia pentaphylla, Cordia alliodora, Bursera simarouba, Attalea cohune*, and *Parmentiera edulis*. The tree suckers were those of the above species plus *Sapindus jabonera, Guazuma ulmifolia, Bombax elipticum, Ceiba pentandra, Lonchocarpus longistylus, Cochlospermum vitifolium, Spondias mombin, Acacia cornigera, Inodes mexicana, Casearia* sp. and *Terminalia* sp. The shrubs formed the bulk of the vegetation and were all regenerated from old root stock. They were *Pithecolobium lanceolatum, Acacia macracantha, Bauhinia unilateralis, Croton glabellus, Robinsonella lindeniana, Jacquinia pungens, Rauvolfia heterophylla, Malphighia glabra, Coccoloba schiendeana, Coccoloba* sp., *Pisonia aculeata, Jatropha urens, Tabernaemontana alba, Mimosa albida, Bixa orellana, Eupatorium odoratum, Triumfetta semitriloba*, and *Bakeridesia galeottii*. Some lower shrubs and annuals that disappear quite early in the succession were *Sida acuta, Croton miradorensis, Solanum torvum, Solanum chloropetalum, Mimosa pudica, Melochia pyrmidata, Hyptis mutabilis, Iresine* sp., and *Salvia* sp. The woody vines were very quick to regenerate following cutting and were very abundant. They were *Tournefortia hirsutissima, Gouania lupuloides, Serjania cardiospermoides, Paullinia tomentosa, Stigmaphyllon lindenianum, Turbina corymbosa, Bigonia unguis-cati, Smilax* sp., and Asclepiadaceae. Annual and non-woody vines were *Dioscorea* spp., Convolvulaceae, Leguminosae, Asclepiadaceae, Passifloraceae, and Marantaceae.

About 30 percent of the vegetation, in the area of Temascal to the east for 10 km, passes through a seral stage similar to this in physiognomy and species composition at least once every 10 years, if not more often. The largest variation between other similar areas and these five plots is in species composition, not in physiognomy.

Throughout the experiments, the shoots in plot P remained in two size groups. About 75 percent of the shoots were in the 10-60 cm size class and were densely shaded during the rainy season. They received light shade during the dry season. They were occupied by colonies of *Pseudomyrmex gracilis mexicana*, founding queens of *Pseudomyrmex ferruginea*, and rarely by auxiliary-units from emergent queen-shoots or by new young colonies. These shoots grow very slowly and are gradually eaten entirely by *Sigmodon hispidus* or die as a result of the cumulative effect of continuous destruction of the shoot-tips by insects. About 25 percent of the shoots were in the 100-250 cm size range and were emergent or canopy members. These were occupied by large colonies of *P. ferruginea* and were not used as standards by the vines in the canopy. During the dry season there was some abandonment of these shoots by auxiliary-units but they were reinvaded when the rainy season started. The colonies of *P. ferruginea* ranged from 500-10,000 workers; most queen-shoots had several auxiliary-shoots. There were at least 150 colonies of *P. ferruginea* and five colonies of *Pseudomyrmex nigrocincta* within these five plots before treatment.

The treatment schedules of the various subplots were as follows:

KA-1: Treatment subplot. Cut to the ground on 1 Oct. 1963. Grazed from 3 Dec. 1963 to 3 May 1964. All *A. cornigera* shoots sprayed with parathion on 26 Oct. and 21 Dec. 1963.

KA-2: Control subplot. As in KA-1, but no treatment.

KA-3: Control subplot. As in KA-2.

K-1: Treatment subplot. Cut to the ground on 1 Oct. 1963. Grazed from 3 Dec. 1963 to 3 May 1964. All thorns clipped on 19 Dec. 1963 and once during the dry season.

K-2: Control subplot. As K-1 except no treatment.

N-1: Treatment subplot. All vegetation except *A. cornigera* cleared to ground level on 10 Oct. 1963. All *A. cornigera* were sprayed with parathion on 26 Oct. 1963 and 14 Nov. 1963. On 3 Apr. 1964 all *A. cornigera* shoots less than 50 cm tall were removed and the thorns of those remaining were clipped. This subplot was grazed from 3 Dec. 1963 to 3 May 1964.

N-2: Control subplot. All vegetation except *A. cornigera* cleared to ground level on 10 Oct. 1963.

O-1: Treatment subplot. As in N-1.

O-2: Control subplot. As in N-2.

P-1: Treatment subplot. Natural vegetation with all thorns of all *A. cornigera* both above and below the canopy clipped on 18 Dec. 1963. Grazed from 3 Dec. 1963 through 3 May 1964.

P-2: Control subplot. Natural vegetation.

In plot KA, the regeneration was apparently unaffected by the parathion treatment. In the two control subplots, most of the shoots of *A. cornigera* remained stunted and gradually became completely shaded. Those that were occupied by colonies invading from the cut shoots and those that developed colonies in situ by the beginning of the rainy season (1964) maintained an emergent or canopy level position. In the treatment subplot, the parathion had no noticeable effect on the high density of founding queens and several colonies moved into the subplot after the spraying from shoots cut outside of it.

In plot K-1, growth was relatively slow in both the treatment and control subplot until shortly before the 1964 rainy season began. Clipping of thorns was extremely effective in destroying the mature colonies remaining after the shoots were cut on 1 Oct. and in preventing new colonies from developing in situ. When new growth was initiated at the beginning of the rainy season, the shoots in the treatment subplot quickly became completely submerged in the general vegetation while about 20 percent of those in the control subplot remained emergent.

In plots N and O growth was relatively slow in both the control and treatment subplots until the beginning of the 1964 rainy season. Parathion was not effective in removing the mature colonies from the treatment subplots because portions of colonies outside of the subplots continued to move into the subplots to reoccupy the shoots vacated by the spray. However, the parathion applications disrupted the occupation sufficiently to allow considerable insect damage to the shoots. When the thorns were clipped and the shoots shorter than 50 cm tall were removed, the occupied shoots outside of the treatment subplots were also removed when they were not part of a control subplot. This produced two ant-free treatment subplots (N-1 and O-1). In the control subplots the shoots less than 50 cm tall were not removed because this might have disrupted the colonies occupying them as auxiliary-shoots. However, these short shoots were not counted in the plot records.

In plot P, growth was relatively slow in both the control and treatment subplots until the beginning of the rainy season. The thorn clipping was extremely effective in removing the mature colonies and founding queens in the shoots. It was aided by the fact that it was the dry season when some of the auxiliary-shoots were abandoned and the very hot sun killed the exposed brood very quickly.

Sigmodon hispidus was present in all plots but did the heaviest damage in plot P and adjacent areas of the same type; it appeared reluctant to forage into the open areas of the other four plots until the rains started and then it did not feed on *A. cornigera* except rarely. Practically all of the insects associated with *A. cornigera* in the Temascal area were found commonly in these five plots. While grazing was relatively light, it was present during most of the cool and dry season; the cattle only occasionally browsed either occupied or unoccupied shoots.

A large part of the behavioral aspects of the bionomics of *Pseudomyrmex ferruginea* were recorded in these five plots. Most of the mating flights that were observed were in the outstanding trees, especially *Attalea cohune*.

Q

Plot Q was a rectangular plot in the brushy pasture 100-250 meters north of El Mocho's house and 10-100 meters west of plots F, G, S and T.

This plot had one control subplot (Q-1) and one treatment subplot (Q-2). At the time that the plot was established (8 Feb.) the area was very heavily grazed. However, the cattle were removed from the area on 3 May and therefore the plot served only to examine the effect of insects on unoccupied shoots (during the rainy season). Since thorn clipping was used to remove the ants, the problem of parathion stimulation was avoided.

This plot was part of a cycle of cutting and burning with frequent heavy grazing. It was last cut in October 1962 but it was not burned at that time. It was on the same 25 acres as plots C, E-I, and S-V. The area of treatment subplot Q-1 was 962 m^2 and the area of control subplot Q-2 was 650 m^2.

In general appearance, plot Q was a very open stand of tree suckers, shrubs, and low herbs with large patches of grass in between. During the dry season, this grass was beaten and grazed down to ground level; during the rainy season, when there were no cattle present, the grass grew to heights of 1-2 m. The tree suckers and shrubs were in the 1-2.5 m height range. *Acacia cornigera* and *Bixa orellana* made up over 75 percent of the woody vegetation. Plot Q had many fewer species of plants than any other plot around El Mocho's house; plot L and M were similar to Q in physiognomy and species composition.

The tree suckers were *Ceiba pentandra, Bursera simarouba, Cordia alliodora, Parmentiera edulis* and *Acacia corngiera*. The shrubs were *Bixa orellana, Eupatorium odoratum, Pisonia aculeata, Jatropha urens, Tabernaemontana alba, Coccoloba schiedeana, Croton glabellus,* and *Cassia bicapsularis*. The annuals and low shrubs were *Sida acuta, Cassia leptocarpa, Croton miradorensis, Solanum chloropetalum,* and *Melochia pyrimidata*. The woody vines were *Bignonia unguis-cati, Turbina corymbosa, Tournefortia hirsutissima,* and *Smilax* sp. There were a few annual vines in the Convolvulaceae and Passifloraceae and two major species of grasses.

Nearly all of the land in the area between Temascal and La Granja that will become a natural pure grass pasture passes through a stage like this one. If the root stocks of the woody plants were removed at this time, and no grazing was allowed for a year, this site would produce a nearly pure grass pasture. This type of plant community becomes increasingly common as cattle become more common.

The shoots of *A. cornigera* were not readily divided into two size groups. Apparently due to the lack of shading of small unoccupied shoots, these shoots live longer in an open plant community than in one with a dense canopy. They eventually become occupied and begin to grow rapidly but the result is rather great variation in height among the shoots. With the exception of a few young colonies developing in situ, the colonies of *P. ferruginea* were mature colonies with 500-5000 workers in them; they often occupied more than one shoot. Before treatment, there were about 50 colonies in plot Q.

On 8 Jan. 1964 all of the thorns in treatment subplot Q-1 were clipped. This treatment was very effective and within a month, all the shoots in the treatment subplot were unoccupied. It was also necessary to remove some of the marginal shoots around the treatment subplot in order to prevent invasion of the clipped thorn shoots from these intact shoots.

The insects commonly found feeding on occupied and/or unoccupied shoots of *A. cornigera* were abundant in plot Q-1. In the clumps of *Bixa orellana, Sigmodon hispidus* was occasionally responsible for the cutting of small unoccupied shoots. Since nearly all of the growth of the plants in plot Q took place after the first rains, cattle were not present at the time of growth.

E, F, G, S, T

These five plots were established in a relatively uniform portion of the brushy pasture 200-400 m north and 100 m west of El Mocho's house.

The purpose of this series of plots was to establish the following types of plots in a single stand of vegetation: 1) an undisturbed plot with the ants removed by parathion (plot S), 2) a plot with all the vegetation except *A. cornigera* cut to ground level and the ants removed by parathion (plot T), 3) a plot with all of the vegetation cleared and the ants removed by destroying the canopies of *A. cornigera* (plot F and E), and 4) a plot in undisturbed vegetation with the ants removed by destroying the canopies of *A. cornigera* (plot G).

This series of plots was part of a cycle of cutting and burning with sporadic light grazing and browsing. It was last cut in July 1962 but it was not burned at that time. During the experiments, cattle were present only between 3 December 1963 and 3 May 1964. The areas in square meters of the various subplots were as follows: S-1, 342; S-2, 448; T-1, 459; T-2, 405; F-1, 157; F-2, 157; G-1, 625; G-2, 225; G-3, 100; E-1, 83; E-2, 167; and E-3, 202.

The general appearance of the area containing the five plots was a dense stand of tree suckers, shrubs and herbs. Most of the vegetation was regenerated from old rootstocks. In September 1963 the general canopy was about 170 cm tall and bound together with a few vines. As the weather became drier during the dry season, the leaf drop from woody plants and the wilting of annuals opened up the vegetation and allowed the sunlight to reach the ground. Yet within a month after the first heavy rains in late May, the vegetation took on again a very closed appearance and by August the canopy had risen to about 250 cm. There were abundant annuals and vines present, apparently due to the absence of cattle which preferred them.

The tree sucker species were the same as in plots K, N, O, P, but they formed a larger portion of the woody vegetation. The same species of shrubs, vines and annuals were present as in plots K, N, O, and P but the proprotions were varied. This type of vegetation represented a seral stage in the same progression of which the above plots and plots C, H, I, U and V were a part, except that the plots S, T, F, G and E represented an intermediate stage between those of plots K, N, O, and P and plots C, H, I, U, and V.

About 10 percent of the shoots of *A. cornigera* were in the 10-70 cm tall size range and were severly shaded except during the peak of the dry season. *S. hispidus* ate many of these shoots during the dry season. About 85 percent of the shoots were in 100-400 cm size range in November 1963. By August 1964 many of the shorter of these shoots had increased 50-100 cm in height. Most of the shoots in the small size range were tenanted by founding queens of *P. ferruginea* or colonies of *Pseudomyrmex gracilis mexicana*. The taller shoots were almost entirely occupied by *P. ferruginea* during the rainy season but there was considerable abandonment of auxiliary-shoots during the dry season, apparently due to the increased high density of *A. cornigera* which resulted in one colony being spread over many shoots. Prior to treatment, there were about 180 colonies of *P. ferruginea* in the five plots. There were also four colonies of *Pseudomyrmex nigrocincta* occupying 11 shoots of *A. cornigera*. There were two tall shoots that had been colonized by *Pseudomyrmex gracilis mexicana* but during the course of the experiments, they were driven from their shoots by *P. ferruginea*. The colonies of *P. ferruginea* were for the most part large, with 1000-15000 workers per colony.

The treatment schedules of the various subplots were as follows:

S-1: Treatment subplot. Natural vegetation, all shoots of *A. cornigera* sprayed with parathion on 4 Nov. and 4 Dec. 1963. Continuous light grazing and browsing until 3 May 1964.
S-2: Control subplot. Natural vegetation and cattle as in S-1.
T-1: Treatment subplot. All vegetation except *A. cornigera* cut to ground on 28 Oct. 1963. *A. cornigera* sprayed with parathion on 4 Nov. and 4 Dec. Cattle present as in S-1.
T-2: Control subplot for T-1. As in T-1 except no parathion used.
F-1: Treatment subplot. All vegetation cut and *A. cornigera* cut at 65 cm on 28 Oct. Canopies of *A. cornigera* piled and burned. Cattle as in S-1.
F-2: Control subplot for F-1. As in F-1 except the canopies of *A. cornigera* left over the stumps instead of burned.
G-1: Treatment subplot. Only *A. cornigera* cut at 65 cm, remainder of vegetation undisturbed, on Oct. 29. Canopies of *A. cornigera* piled and burned. Cattle as in S-1.
G-2: Treatment subplot. As in G-1.
G-3: Control subplot. As in G-1 except that the canopies of *A. cornigera* were left over the stumps instead of being destroyed.
E-1: Treatment subplot. All vegetation cut and *A. cornigera* cut at 65 cm on 18 Nov. Canopies of *A. cornigera* piled and burned. Cattle as in S-1.
E-2: Treatment subplot. As in E-1.
E-3: Control subplot for E-1 and E-2. As in E-1 except that canopies of *A. cornigera* left over the stumps instead of being destroyed. On 23 Mar. added a queen-unit to each unoccupied shoot (10 shoots).

In plot S, the parathion treatment was relatively effective in removing *P. ferruginea* but due to the close proximity of colonies outside of the plot, there was a relatively rapid reinvasion of these shoots. It was in this plot that parathion stimulation was most noticeable. The same situation occured in plot T.

In plot F, there were relatively few ant colonies around the margins and the treatment subplots thus stayed relatively free of *P. ferruginea.* On 23 March a queen-unit in the form of a cut queen-shoot was added to each of the stumps in the control subplot in which the transfer of the unit from the old cut shoot had not been successful. All 10 of these queen-units became established. Toward the end of the dry season there was a rapid invasion of the shoots in the west side of treatment subplot E-1 from two large queen-shoots growing outside of the subplot.

Fourteen adult and yearling cattle were present in all five of these plots until 3 May 1964. Most of the animals browsed and grazed independently of the others; they were rather evenly dispersed over the 25 acre area that includd plots F, G, S, and T, E and C, H, I, U and V. All the common insects that fed on *Acacia cornigera* were present in these plots; *Coxina hadenoides* was especially abundant in plots F and G. *S. hispidus* was abundant only in plots S and G; this appeared to be associated with the high cover of these plots.

C, H, I, U, V

These five plots were arranged along the sides of the water pipeline that ran northeast from El Mocho's house. They were 200-1000 m east of plot Q and 200-300 m north of the Temascal-La Granja highway. Within each plot, rectangular subplots were established. Plot U is shown in Figure 51.

The employment of these five plots was to use the various treatments (parathion, thorn clipping, stump regeneration) in a thick stand of woody regeneration that was browsed by cattle and had a high density of *A. cornigera.* The cattle were removed from the plots on 3 May so that the major portion of the growth that took place was free from cattle foraging.

The regeneration in these five plots before treatment was of the same type of cycle as in plots K, N, O, P, E, F, G, S, and T, but was older. It was last cut to the ground in 1962 and according to the owner was lightly burned at that time; it must have been a light fire since there were many large colonies of *P. ferruginea* present in late 1963. The areas of the various

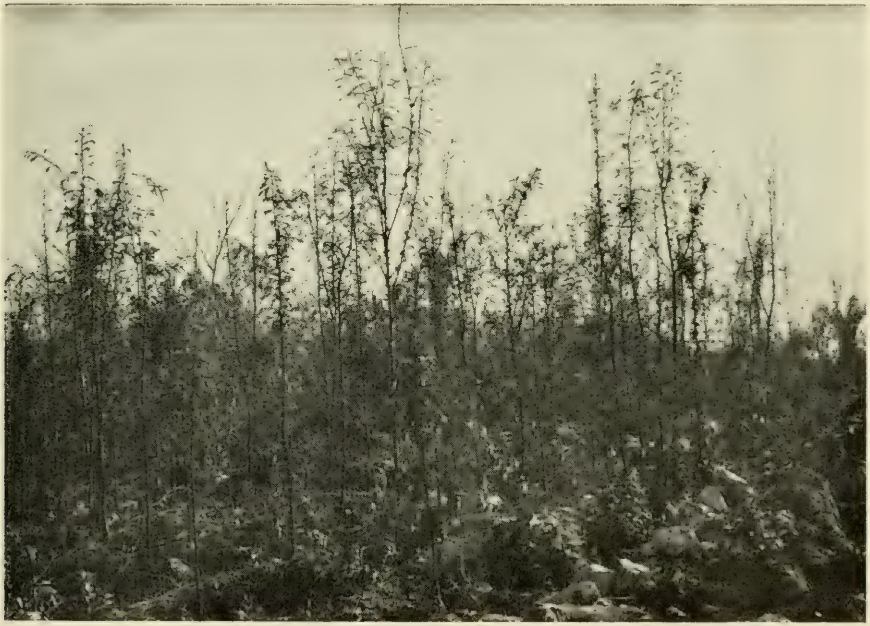


FIG. 51. General aspect of treatment subplot U-1 in January 1964. Leaf drop has begun on the shoots of *Acacia cornigera* but the low sucker regeneration of many species of plants under the *A. cornigera* is in full leaf though growing slowly. Before the area was sprayed, there were about six colonies of *P. ferruginea* in the shoots immediately visible in the photograph. Each colony was large with auxiliary-shoots.

subplots in square meters were as follows: V-1, 1200; V-2, 1200; U-1, 750; U-2, 720; H-1, 2,025; H-2, 2,005; H-3, 1,895; I-1, 300; I-2, 325; I-3, 250; C-1, 500; C-2, 460; and C-3, 620.

In general appearance before treatment, these plots contained a very dense stand of woody regeneration that was interlaced with woody and annual vines. There were relatively few low shrubs. As the dry season progressed, the stand opened to such an extent that one could walk through it but by August 1964 it was nearly impassible except along old cattle trails. *A. cornigera* formed such a large part of the canopy that from a distance of 500 m, it looked like a pure stand. The canopy was 2-3.5 m high and cast a very heavy shade during the rainy season. There were occasional old trees 30-50 meters tall that were remnants of the old forest that was on the land 20 years earlier. Though the land was relatively flat, there were occasional limestone knolls with a very distinctive xerophytic vegetation; *A. cornigera* did not grow on these and no knolls were contained in the subplots.

The scattered old trees were *Ceiba pentandra, Sapindus saponaria, Enterolobium cyclocarpum, Bursera simarouba, Tabebuia pentaphylla,* and other species. The limestone knolls were covered with *Bombax ellipticum, Inodes mexicana,* climbing cacti, cycads, Marantaceae, Acacanthaceae, succulent leaved xerophytic herbs, Agavaceae, and terrestrial bromeliads. On the level ground, there were tree suckers of the trees listed above, except *Bombax ellipticum,* plus *Piscidia communis, Cochlospermum vitifolium, Cordia alliodora, Spondias mombin, Attalea cohune,* and *Acacia cornigera.* In one of the arroyos there were a few *Acacia macracantha* and *Acacia chiapensis.* The common shrubs in the plots were *Solanum umbellatum, Croton glabellus, Jatropha urens, Casimiroa edulis, Cassia bicapsularis, Esenbeckia berlandieri, Buettneria aculeata, Eupatorium odoratum, Jacquinia pungens,* and other unidentified species. The woody vines were *Turbina corymbosa, Tournefortia hirsutissima, Bignonia unguis-cati, Gouania lupuloides, Serjania* sp., *Cissus* sp., and various species of Leguminosae, Asclepiadaceae, and Convolvulaceae. The annual vines were *Dioscorea* spp., Leguminosae, Convolvulaceae, and Asclepiadaceae. Small openings had several species of grasses and herbs growing in them.

The stand in which these five plots were established represents an older seral stage in the progression and cycle represented by plots K, N, O, P, E, F, G, S, and T. After another year of growth this stand of vegetation would have begun to open up underneath as had happened in the case in plots D and R.

Better than 95 percent of the shoots of *A. cornigera* were canopy members or emergent at the time the plots were established. When the vegetation was cleared in some of the plots a few old stumps produced new sucker shoots. The shoots were old enough to respond strongly to the cool and dry season by cessation of most growth except the production of axillary tufts of leaves and flowering branches. The colonies of *P. ferruginea* had 1000-15,000 workers in them and occupied 3-15 shoots. There were no colonies of *Pseudomyrmex nigrocincta*; two nearly dead tall shoots had colonies of *Pseudomyrmex gracilis mexicana.* Most of the *P. gracilis mexicana* colonies in these plots lived in the hollow stems of *Buettneria aculeata.* During the dry season there was a 10-30 percent abandonment of auxiliary-shoots by *P. ferruginea.* There were approximately 120 colonies of *P. ferruginea* in the five plots before treatment.

The treatment schedules for the various subplots were as follows:

V-1: Treatment subplot. Natural vegetation, all *A. cornigera* sprayed with parathion on 30 Oct. and 21 Nov. Light grazing and browsing until 3 May 1964 when they were removed by the owner.

V-2: Control subplot for V-1. As in V-1 except no parathion used.

U-1: Treatment subplot. All vegetation except *A. cornigera* cut to ground on 20 Oct. and all shoots of *A. cornigera* sprayed with parathion on 31 Oct. and 21 Nov. Cattle as in V-1.

U-2: Control for U-1. As in U-1 except no parathion used.

H-1: Treatment subplot. All vegetation cut on 17 Oct., *A. cornigera* cut at 65 cm and canopies piled and burned. *A. cornigera* sprayed with parathion on 30 Oct. and thorns clipped on 13 Mar. Cattle as in V-1.

H-2: Treatment subplot. As in H-1 except that thorns not clipped.

H-3: Control for H-1 and H-2. As in H-1 except that canopies of *A. cornigera* left over their stumps and no parathion or thorn clipping.

I-1: Treatment subplot. *A cornigera* cut at 65 cm and canopies piled and burned on 18 Oct. Cattle as in V-1.

I-2: Treatment subplot. As in I-1.

I-3: Control subplot. As in I-1 except canopies left over their stumps.

C-1: Treatment subplot. *A. cornigera* cut at 65 cm and canopies piled and burned on 5 Jan. Thorns clipped on 14 Mar. Cattle as in V-1.

C-2: Treatment subplot. As in C-1 except thorns not clipped.

C-3: Control subplot for C-1 and C-2. As in C-1 except thorns not clipped and what appeared to be a queen-unit added to each shoot on 14 Mar.

In plot V the parathion spray was only moderately effective but still reduced the colony size of most colonies. There was a rapid initial reinvasion of the treatment subplot from large colonies outside of the subplot but, judging by the amount of insect damage that took place in the 1964 rainy season in the treatment subplot, the numbers of workers per shoot still remained much lower than normal. If the acacias outside of the treatment subplot had been removed before the treatment, it appeared that the parathion treatment could have been permanently effective.

In plot U the same thing happened as in plot V except that the reinvasion was slower but by the 1964 rainy season the numbers of workers on the shoots were back to normal.

In plot H and I the treatment was very effective in removing the colonies of *P. ferruginea.* The parathion spray used in plot H was not necessary but it seemed to be so at the time because of the few workers left when the shoot was cut. The thorn clipping in subplot H-1 prevented the development of young colonies in situ; in plots H-2, 30 of these colonies had developed by 5 Aug. The long thin subplots in plot I were very close to *A. cornigera* that were not cut. Therefore, abandonment to, and reinvasion from these plants considerably complicated the degree of occupation of shoots.

In plot C, the treatment was effective. However, the damage sustained by the unoccupied shoots in the control subplot before the queen-units were added on 14 Mar. caused a number of these to grow very poorly or not at all even after they were occupied. A further complication was that apparently about one-half of the supposed queen-units were auxiliary-units and therefore did not persist on the shoots.

All of the common insects that fed on *Acacia cornigera* were found in these plots. When cattle were present, they browsed and grazed in a highly dispersed pattern. They fed very rarely on *A. cornigera,* irrespective of whether it was occupied or not. However, it was in this area that the cattle were frequently observed browsing *A. cornigera* during the cool season when it was unoccupied due to lowered worker activity at the time. *S. hispidus* was occasionally seen in these plots but there were almost no shoots present that were small enough for it to feed on.

J

Plot J was a rectangular plot in the middle of a corn field 800 m south of Señor Torrealva's house. His house was on the north side of the Temascal-La Granja highway at Parada Pochota which was 7 km east of Temascal.

The site of plot J was chosen because it was on red laterite soil and because of the very young vegetation that was present following the use as a corn field. The plot was established after the soil had begun to dry out and the cool season had set in. While this soil had never been plowed, the vegetation had been burned severely during the 1963 dry season and was cut very close to the ground in July of 1963. It had been cleared for a corn field in 1960. The land-use schedule was that cattle were excluded and corn planted when the first rains fell. By November, the cattle were allowed to graze in the regeneration until the end of the following dry season. The total area of the corn field was about 15 acres and plot J was roughly in its center. Treatment subplot J-1 had an area of 200 m^2 and control subplot J-2 had an area of 180 m^2.

In December 1963 the general aspect of the field was one of nearly bare red laterite littered with corn stalks, and a very sparse cover of shrub suckers and vines. There were a few scattered trees. The field was surrounded on three sides by extremely dense regeneration from previous corn fields; this vegtation was about 2.5 m tall and composed of Malvaceae, Leguminosae, and Sterculiaceae. There were very few *A. cornigera* in it. In plot J the *A. cornigera* were 5-35 cm tall and none were occupied; nearly all of the new thorns had founding queens in them.

The trees in and around plot J were *Acromia mexicana, Inodes mexicana,* and *Attalea cohune.* There were suckers of the above three species plus *Acacia cornigera, Byrsonima crassipes, Curatella americana* and *Quercus* sp. The shrub species were *Croton glabellus, Bauhinia ungulata, Mimosa albida, Calliandra houstoniana, Cassia bicapsularis, Conostegia jalapensis,* and *Coccoloba* sp. There were a number of prostrate herbs and non-woody vines. During the winter, grasses were not evident but during the rainy season they sprouted in great abundance.

When the 1964 rainy season began, the entire corn field was fenced off. It was cleared and planted except for the plot. The vegetation in plot J had grown very thick and lush by the end of July. Most of the vegetation consisted of grasses and herbaceous annuals. The woody shrub and tree suckers constituted a minor part of the vegetation. The vegetation was so dense that there was standing rain water on the soil under it even on the hottest and driest days. All shoots on *A. cornigera,* except for three that had young colonies of *P. ferruginea* that had developed in situ, were well below the canopy and received almost no sunlight.

The treatment schedule of the two subplots was as follows:

J-1: Treatment subplot. Undisturbed vegetation with all *A. cornigera* sprayed with parathion on 1 Dec. thorns clipped on 15 Jan. Cattle present until 22 May.

J-2: Control subplot. As in L-1 except that no parathion or thorn clipping.

The parathion had no noticeable effect on the founding queen population. The thorn clipping was used to keep new colonies from developing in the shoots. When the final recording was made, the thorns in the control subplot were opened. Many of them contained young colonies with 5-20 workers but only three had a colony large enough to occupy the outside of the shoot.

The insects commonly associated with *A. cornigera* were present in plot J but at very low densities. The cattle browsed and trampled the area severely during the dry season but rarely ate foliage of *A. cornigera*. *Sigmodon hispidus* was not present in the plot during the dry season but was extremely common there during the rainy season. It did not feed on *A. cornigera* at that time.

L, M

These two plots were established in the brushy pasture 50-100 m south of the Temascal-La Granja highway across from Señor Torrealva's house and 50 m southeast of the largest *Ceiba pentandra* in the area (La Pochota).

As can be seen in Figure 52, these two plots had very open vegetation. The site was uncomplicated by the presence of large colonies remaining after the last clearing; the site was severely burned in May 1963. It received heavy grazing throughout the rainy season but the cattle were removed about the time that the experiments started (Oct.); picketted Indian horses remained, however. The result of the heavy grazing during the rainy season was that there were a large number of unoccupied but living shoots in the 30-60 cm size range in October; in a neighboring area that had been burned at the same time but not grazed, nearly all of the shoots were severely stunted and nearly dead. During the course of the experiment, young colonies developed in most of the shoots in the two plots while none developed in the adjacent area.

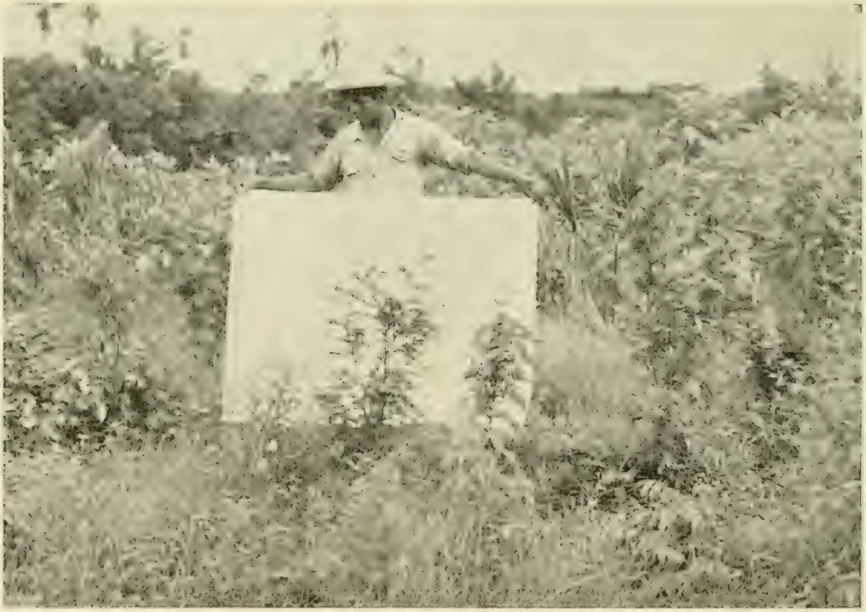


FIG. 52. General aspect of treatment subplot M-1 in November 1963. The shoot of *Acacia cornigera* directly in the center of the sheet is occupied by a small colony of *P. ferruginea* that had developed in situ. It has an undamaged uppermost shoot tip. The shoot in front of the right-hand portion of the sheet contains only founding queens of *P. ferruginea*. It also has an undamaged uppermost shoot tip but is festooned with vines and has produced much less foliage than the occupied shoot.

The area included in the two plots was used as a corn field in 1962 and the two preceeding years. It had a species composition and physiognomy rather similar to plot J. The areas of the four subplots in square meters was as follows: M-1, 600; M-2, 600; L-1, 300; L-2, 525.

The general aspect of the plots was one of a very open canopy, with woody shrub and tree suckers scattered on low grass. By August 1964 the grass was 40-100 cm deep and there was considerable herbaceous growth. It was not until several months after the *A. cornigera* became occupied that they began to appear as emergents above the heights of other species of woody plants.

The tree suckers were *Acromia mexicana, Inodes mexicana, Ateleia pterocarpa, Coccoloba schiedeana, Acacia cornigera, Guazuma ulmifolia,* and *Cordia alliodora.* The annual and woody shrubs were *Helicteres guazumaefolia, Croton glabellus, Pithecellobium lanceolatum, Jatropha urens, Cassia bicapsularis, Bauhinia ungulata, Bauhinia unilateralis, Solanum torvum, Cordia ferruginea, Mimosa albida, Mimosa pudica, Tabernaemontana alba,* and *Jaquinia pungens.* Once the cattle had been removed, the following vines became common: *Passiflora foetida, Rhabdademia paludosa, Stigmaphyllum lindenianum,* and *Ipomoea* sp. There were a number of species of grasses and sedges.

These two plots were representative of the second year of the seral progression of which plot J represented the first year. The land-use pattern, cornfield to fallow and back again to cornfield, is very common in the Temascal area. These two plots on a soil intergrade zone between the black soils and red laterites.

At the beginning of the experiment, the *A. cornigera* were occupied by founding queens and an occasional small colony with 20-50 workers. By the end of July 1964, most of the untreated shoots had developed a young colony in situ with 100-1600 workers in it. In several cases, there were auxiliary-shoots present as well. At the beginning of the experiment there were four shoots along the margins of the area that were occupied by *Pseudomyrmex gracilis mexicana.* By late July 1964 three of these colonies had been removed by *Pseudomyrmex ferruginea* and one by *Pseudomyrmex nigrocincta.*

The treatment schedules for the various subplots were as follows:

M-1: Treatment subplot. Natural vegetation, all *A. cornigera* sprayed with parathion on 28 Oct. and on 6 Dec. Thorns clipped on 20 Apr.
M-2: Control subplot for M-1. As in M-1 but no parathion or thorn clipping.
L-1: Treatment subplot. Natural vegetation, all *A. cornigera* thorns clipped on 11 Dec.
L-2: Control subplot for L-1. As in L-1 but no thorn clipping.

All of the insects commonly found associated with *A. cornigera* were very common in this plot. *Diplotaxis denigrata* was especially common. Cattle were not allowed free browsing in the two plots, but Indian horses and burros were occasionally tethered on the acacias. *Sigmodon hispidus* cut a few shoots in these plots during the dry season.

A, D, R

These three rectangular plots were established in the five year old regeneration 50-300 m south of Señor Torrealva's house and 100-150 m west of the plots L and M.

Before treatment, these three plots contained a five year old stand of fallow regeneration after use for a cornfield in 1959. It was lightly grazed and browsed throughout this regeneration. There was a closed canopy of young trees at about 3-4 m above ground level. While this canopy was interlaced with woody vines, the understory was sufficiently clear to walk through with ease. It was hoped that the plots would clarify some aspects of the effects of shading on *A. cornigera.* The areas in square meters of the various subplots were as follows: R-1, 800; R-2, 600; D-1, 120; D-2, 120; D-3, 110; A-1, 225; and A-2, 550.

There were a few large trees remaining from the forest that covered the site before it was cleared in the late 1940's. The canopy at 3-4 m height cast a very heavy shade during the rainy season and the plants growing at ground level were either shade tolerant species or ones such as *A. cornigera* which occupy open sites and show abnormal growth in heavy shade. The canopy member or emergent *A. cornigera* were fully developed shoots that had maintained their position in the canopy while the regeneration of the vegetation occurred. There were a few shoots of *A. cornigera* that developed later and grew up into vacancies in the canopy once they became occupied; these were usually auxiliary-shoots to canopy members or emergent queen-shoots.

The large trees were *Ateleia pterocarpa, Casearia sylvestris, Attalea cohune, Tabebuia pentaphylla, Cecropia obtusifelia,* and *Quercus* sp. The main canopy was made up of *Cordia ferruginea, Vitex pyramidata, Bauhinia ungulata, Acacia cornigera, Guazuma ulmifolia, Helicteres guazumaefolia, Cochlospermum vitifolium,* and *Bakeridesia galeottii.* The woody vines were in the Leguminosae, Asclepiadaceae, Sapindaceae, and Bignoniaceae.

Two size classes of *A. cornigera* were present. In plot R the canopy member and emergent shoots were omitted in the plot consideration because of the impossibility of spraying these 5-9 m tall shoots with the apparatus available. The members of the smaller size class were those used in the experiments; these plants probably would never have reached maturity unless the vegetation was cleared. These smaller plants were occupied by founding queens of *Pseudomyrmex ferruginea, P. nigrocincta* and *P. gracilis mexicana.* There was an occasional small colony and some of the shoots were occupied as auxiliary-shoots to the canopy member or emergent shoots. In the other two plots, the stumps of the cut taller shoots were used as the experimental shoots. The canopies of the taller shoots had colonies of *P. ferruginea* in them that ranged from 1,000-15,000 workers.

The treatment schedule for the various subplots was as follows:

R-1: Treatment subplot. Natural vegetation, all *A. cornigera* below the canopy sprayed with parathion on 9 Dec. 1963. Site very lightly grazed by cattle throughout the experiment.
R-2: Control subplot for R-1. As in R-1 except no parathion used.
D-1: Treatment subplot. Natural vegetation, all canopy member or emergent shoots of *A. cornigera* cut at 65 cm and the canopies piled and burned on 10 Dec. Cattle as in R-1.
D-2: Treatment subplot. As in D-1.
D-3: Control subplot for D-1 and D-2. As in D-1 except that canopies of *A. cornigera* left over their stumps.
A-1: Treatment subplot. All vegetation cut on 25 May 1964 and *A. cornigera* cut at 65 cm. Canopies of *A. cornigera* plied and burned. Cattle browsed and grazed the area slightly more heavily than plots R and D.
A-2: Control subplot. As in A-1 except that canopies of *A. cornigera* left over their stumps.

The spraying in plot R was relatively ineffective since founding queens moved back into the shoots and the canopy member and emergent shoots replaced the destroyed auxiliary-units. However, the low growth rates in these two subplots helped to elucidate the effect of shade on *A. cornigera.*

The regeneration in plot D became very complicated because of the close proximity of uncut shoots to the cut shoots; auxiliary-units from these colonies moved into a number of the new regeneration from the stumps.

In plot A, the tall shoots around the treatment subplot were removed when the treatment subplot was established; this prevented movement into the area by auxiliary-units. In the control subplot the large units moved into new shoots and there was very effective occupation.

All of the insects commonly associated with *A. cornigera* were seen in plot D and A; since the emergent and canopy member *A. cornigera* in plot R were not removed, the canopy remained intact and the shade dense and this appeared to reduce the numbers of insects found on *A. cornigera.* Their damage was however frequently present. Cattle did not browse *A. cornigera* except when the tall shoots were cut. *Sigmodon hispidus* was not seen in the plots nor were shoots cut by it in the plots.

DATA FROM SUBPLOTS. When comparing the growth and development of unoccupied and occupied shoots of *Acacia cornigera,* the following parameters were recorded in the subplots: mortality, height increment, emergence, invasion by vines, condition, presence of phytophagous animals, thorn production, leaf production, and total biomass production. All of these parameters were recorded during the study for at least one pair of treatment and control subplots. The data from these recordings is examined in this section. In the 22 plots containing 50 subplots, the height increments and condition of the shoots were recorded at intervals of a month or more. The plots were established between October 1963 and May 1964. The majority were followed during the 1964 dry season and the first two months of the 1964 rainy season. The data from these plots are examined by comparisons between subplots (Tab. 4-9, 14-21). Since most of the subplots were mapped, and the individual shoots numbered, and since the presence of workers on the surface of the shoot was recorded in each case, it was possible to extract a second set of height increment and condition data from the subplots. This consists of two groups of shoots, one of which was unoccupied during the interval between two recordings, and the other occupied. The data from the groups are examined by comparisons within the plots taken as a whole (Tab. 10-13, 22-26). In these comparisons, both the subplot pairs or triplets, and the groups of occupied and unoccupied shoots are arranged as groups of suckers from stumps that were cut as part of the experimental program (Tab. 4-6, 10-11, 14-17, 22-24) and groups of naturally existing shoots (Tab. 7-9, 12-13, 18-21, 25-26).

Height increment. Significance. The height increment is one of many possible indicators of the amount of growth that has taken place over a period of time. *A. cornigera* is a plant of disturbed sites. In order to obtain sufficient sunlight for growth, it must maintain its position in or above a rapidly rising canopy.

A positive height increment can only occur when the uppermost shoot tip is undamaged. A few days to several months are required for a new vertically lengthening shoot tip to surpass a damaged terminal shoot tip. Therefore, the height increment is also a function of the amount of time that the shoot tip remains undamaged. For example, if a shoot has a mean height increment of 2.5 cm per day for a two month period, it is very unlikely that the uppermost shoot apex has been damaged by any agent during the two month period.

Negative height increments occurred on some heavily occupied shoots during the later portion of the rainy season. In this case, the terminal 30-150 cm of the main axis was not able to support the weight of the swollen-thorns and became bent. Figure 19b shows a section of such a central axis. Shoots are also shortened by having the terminal 3-10 cm of the succulent shoot tip eaten off by insects such as *Pelidnota punctulata, Coxina hadenoides,* and tettigoniid grasshoppers. Large negative height increments occur on unoccupied shoots, when the cerambycid *Onicideres poecila* cuts off the shoot, or the rodent *Sigmodon hispidus* eats the shoot. The weight of the flowers and flowering branches produced on heavily defoliated unoccupied shoots sometimes causes the central axis to bend and thereby shortens the height by a few centimeters.

Because of the frequently curved or slanted life form of the shoot, the length of shoots over 100 cm tall is often greater than the height of the shoot. Suckers from cut stumps in only slightly shaded sites grow vertically without bending during the first 9-12 months of regeneration. In these cases, the length rather than the height of the shoot is of importance and is recorded; this removes the variation associated with the height on the stump at which the sucker originated.

Even among a group of even-aged shoots on the same site, there is considerable individual variation in height (or length) increment rate. This can

TABLE 3. The air temperatures recorded at he Temascal weather station of the Comicion del Papaloapan, during the period 1 Jul. 1963 through 31 Jul. 1964 (unpublished). All values are reported in degrees C. The three sets of underlined values represent the location of the cool season.

	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.
$\bar{X}$ daily maxima (° C)	31.4	32.0	30.8	29.2	28.4	24.1	24.2	25.5	29.4	32.2	33.2	31.3	30.4
$\bar{X}$ daily minima (° C)	22.7	22.8	22.7	21.4	19.5	16.5	15.7	17.0	19.7	22.0	23.3	22.7	22.7
Days with maxima 24° C or less	0	0	0	0	3	16	15	9	3	1	0	1	0

be readily seen in the high standard deviation values in the tables for height increment. The major portion of this variation is associated with the activity of the occupying ant colony (or fraction thereof), the frequency of attack of the plant by phytophagous animals, the size of the parent root stock, and the time of year (temperature and rainfall effect on physiological growth rates). Individual inherent variation in growth rate is present but plays a minor role compared to the above four factors. It appears that there is little variation in growth rates of undamaged shoot tips of vertically lengthening branches on occupied shoots over 100 cm tall at a given time of year.

Subplot length increment records for suckers and stumps. In table 4, the length increments are recorded for nine plots that contained 24 subplots. The shoots were all suckers regenerating from stumps cut as part of the experimental program. The length increment is that which accrued during the first part of the 1964 rainy season. They were cut before the cool season in 1963 (plots H, I, F, G, and E), during the cool season 1963-1964 (plots D and C), or during the 1964 dry season (plots A and B). Parathion was used only during October and/or November in the treatment subplots H and I. Thorn clipping was used in treatment suplots H-1 and C-1 to insure unoccupied shoots. The original removal of the canopies was the only treatment used in subplots I-2, G-1, E-1, E-2, C-2, B-1, and A-1.

Of the 17 treatment-control contrasts between subplots in table 4, 11 of the pairs have a highly significant difference in mean height increment, one is significantly different, and five are not significantly different. On each of the comparisons, significant Z values pertain to higher increment values in the control subplot. High negative Z values are the result of the same factors responsible for negative Z values that are not significant at either the 5 or 1

TABLE 4. The length increment data for suckers from stumps treated as subplots. The majority of the days in the time intervals occur in the 1964 rainy season. In the "ants removed by" column, R=removal of the colony, P=spraying with parathion, T=clipping the thorns, and C=control subplot. Where more than one treatment was used, the order of the letters indicates the order of treatment. The fraction in the "Begin" and "End" column has as its numerator the number of occupied shoots in the subplot and as its denominator the total number of shoots in the subplot. The plots in Tables 4 through 28 were recorded during daylight hours. "Begin" signifies the count at the beginning of the time interval and "End" signifies that at the end of the interval. The $\overline{X}_o$ and s.d.$_o$ columns contain the mean length, and its standard deviation, of the shoots in the subplots at the beginning of the interval. The $\overline{X}_{inc}$ and s.d.$_{inc}$ columns contain the mean length increment and its standard deviation over the time interval. The Z values are computed between the mean growth increments in the treatment and control subplots. Significant Z values are indicated by an asterisk, and highly significant Z values are indicated by a double asterisk. Large negative Z values are not asterisked for reasons explained in the text.

			Occupied Total		Length		Increment		
Sub-plot	Ants removed by	Time interval	Begin	End	$\overline{X}_o$ (cm)	s.d.$_o$ (cm)	$\overline{X}_{inc}$ (cm)	s.d.$_{inc}$ (cm)	Z values
A-1	R	25 May-	0/42	0/42	0.00	0.0	6.23	5.6	7.516**
A-2	C	16 Jun.	29/29	26/29	0.00	0.0	30.96	17.1	
A-1	R	16 Jun.-	0/42	1/42	6.23	5.6	10.23	9.8	8.808**
A-2	C	3 Aug.	26/29	29/29	30.96	17.1	72.86	37.4	
B-1	R	23 May-	3/53	7/53	5.15	6.6	31.15	25.7	4.250**
B-2	C	17 Jun.	41/47	44/47	14.36	11.3	55.83	16.2	
B-1	R	17 Jun.-	7/53	19/53	36.30	28.2	44.73	73.2	3.318**
B-2	C	7 Aug.	44/47	45/47	70.19	26.4	92.19	69.6	
C-1	R, T	27 May-	2/20	6/20	35.25	40.2	26.10	54.2	1.212
C-2	R		2/19	5/19	35.15	32.8	28.78	60.7	0.995
C-3	C	6 Aug.	13/31	14/31	32.16	39.8	47.19	69.2	
D-1	R	25 May-	3/9	3/9	30.11	29.5	36.33	53.9	−0.058
D-2	R		6/12	7/12	28.25	25.1	36.16	53.2	−0.072
D-3	C	28 Jul.	4/19	3/19	47.52	53.9	34.94	40.3	
E-1	R	10 Jun.-	4/29	6/29	58.55	45.5	12.72	42.9	3.515**
E-2	R		2/24	4/24	32.16	31.5	1.41	17.7	19.049**
E-3	C	7 Aug.	21/21	21/21	96.33	40.3	116.09	22.1	
F-1	R	24 Apr.-	19/42	26/42	30.38	24.6	30.57	49.6	0.884
F-2	C	6 Jul.	25/40	29/40	32.37	23.4	39.32	39.6	
G-1	R	24 Apr.-	1/18	6/18	18.27	18.8	7.00	23.4	4.703**
G-2	R		5/26	9/26	33.20	21.5	29.07	39.2	1.982*
G-3	C	6 Jul.	10/24	19/24	32.20	21.5	51.12	39.4	
H-1	R, P, T	10 Jun.-	0/43	0/43	15.18	15.4	0.47	7.1	10.344**
H-2	R, P		2/66	32/66	25.12	20.6	8.16	19.0	8.803**
H-3	C	5 Aug.	7/72	64/72	83.48	46.4	74.63	60.9	
I-1	R	10 Jun.-	13/38	15/38	33.13	46.5	37.36	43.5	3.593**
I-2	R		8/32	8/32	38.15	58.4	19.12	40.1	5.459**
I-3	C	5 Aug.	27/39	27/39	52.79	45.9	83.00	66.0	

TABLE 5. As in Table 4 except that the majority of the days in the time intervals occur in the dry season.

Sub-plot	Ants removed by	Time interval	Occupied Total		Length		Increment		Z values
			Begin	End	$\bar{X}_o$ (cm)	s.d.$_o$ (cm)	$\bar{X}_{inc}$ (cm)	s.d.$_{inc}$ (cm)	
B-1	R	29 Apr.-	0/53	3/53	0.00	0.0	5.15	6.1	4.898**
B-2	C	23 May	47/47	41/47	0.00	0.0	14.36	11.3	
C-1	R, T	14 Mar.-	2/20	2/20	16.25	13.8	19.00	27.4	0.387
C-2	R		1/19	2/19	15.05	13.4	20.10	24.2	0.236
C-3	C	27 May	1/31	13/31	10.67	14.5	21.49	10.6	
D-1	R	10 Dec.	0/9	3/9	0.00	0.0	30.11	29.5	1.101
D-2	R		0/12	6/12	0.00	0.0	28.25	25.1	1.347
D-3	C	25 May	19/19	15/19	0.00	0.0	47.52	53.9	
E-1	R	23 Mar.-	0/29	4/29	16.72	13.2	41.83	37.9	2.887**
E-2	R		0/24	2/24	18.37	15.4	13.79	22.5	6.958**
E-3	C	10 Jun.	11/21	21/21	26.66	22.7	69.67	30.2	
F-1	R	6 Jan.-	11/42	19/42	22.00	13.5	8.38	17.4	1.664*
F-2	C	24 Apr.	27/40	25/40	17.60	13.6	14.77	17.4	
G-1	R	6 Jan.-	2/18	1/18	11.16	14.3	7.11	7.1	—1.114
G-2	R		10/26	5/26	23.30	15.4	9.90	14.6	—1.818
G-3	C	24 Apr.	15/24	10/24	29.41	14.3	3.79	12.1	
H-1	R, P, T	11 Mar.-	0/43	0/43	15.34	13.0	—0.16	9.3	9.508**
H-2	R, P		0/66	2/66	24.12	16.6	1.00	13.6	9.144**
H-3	C	10 Jun.	65/72	67/72	43.80	21.1	39.68	33.5	
I-1	R	13 Mar.-	12/38	14/38	12.63	19.0	8.89	15.2	0.003
I-2	R		0/32	7/32	13.84	16.8	1.53	11.3	2.585**
I-3	C	18 Apr.	33/39	29/39	21.71	23.4	8.90	12.7	
I-1	R	18 Apr.-	14/38	14/38	21.52	30.4	11.61	18.8	2.060*
I-2	R		7/32	8/32	15.37	21.8	22.78	32.6	—0.076
I-3	C	10 Jun.	29/39	27/39	30.61	30.6	22.18	25.8	

percent level. In treatment subplot G-2 and F-1, the large length increment (small Z value) was due to the presence of several vigorous shoots occupied by large ant colonies. In plot D and C, there were several heavily occupied shoots in each treatment subplot and a number of dead stumps in each control subplot. A major portion of the variance of the length increments in all of the subplots in table 4 was due to 1) the presence of unoccupied shoots in treatment subplots, 2) unoccupied shoots in control subplots, 3) dead shoots that were killed by *Chrysobothris* sp., near *multistigmosa* and continuous defoliation by phytophagous insects, 4) damage to shoot tips by *Coxina hadenoides* and *Pelidnota punctulata*, and 5) variable occupation of shoots in the control subplots during the period of the height increment.

In table 5, the length increments are recorded for eight of the nine plots in table 4. The length increment was for the most part that which accrued during the 1964 dry season. Of the 16 treatment-control contrasts, six of the pairs have a highly significant difference in mean height increment, two were found to be significantly different, and eight were not significantly different. The low Z values obtained in the contrasts in plot F and I were associated with the presence of 1) lightly occupied shoots in the control subplots, 2) occupied shoots in the treatment subplots, 3) apparently lowered replacement rates of the shoot tips destroyed by *Coxina hadenoides* (due to the dry season), and 4) dead shoots in the control subplots. The low Z values obtained in the eight contrasts that did not show significant differences were associated with the same factors, but the presence of occupied shoots in treatment subplots, and the lowered rate of shoot tip replacement by all shoots, contributed the most to the reduction of differences between the control and treatment subplots.

In table 6, the length increments are recorded for 7 of the nine plots discussed in table 4. The length increment was for the most part that which accrued during the cool season, and the period associated with the end of the 1963 rainy season and the beginning of the 1963-1964 dry season. The 24 contrasts must be divided into two groups. The majority (18) are contrasts of treatment subplots with control subplots in the same manner as presented in tables 4 and 5; they are possible because individual records were kept for each shoot. Four of these contrasts have highly significant differences in mean length increment, one has a significant difference, and 13 do not show significant differences. In the case of the other six contrasts, the individual length increment can not be associated with the individual shoot. The mean lengths of the shoots in the subplots can be contrasted at the start of the interval and at the end of the interval. Four of these pairs of contrasts (plot H) have highly significant differences both at the beginning and end of the interval, and show increases in the Z value over the interval. The differences in mean length increment among the subplots in plot H appear great enoufih during the period 19 Nov.-26 Dec., so that significantly different length increments probably occurred. During the period 26 Dec.-11 Mar., it is doubtful that significantly different length increments occurred. In the contrast of subplot I-1 with I-3, the Z value changed from a negative number to a significant value over the time interval. In the contrast of subplot I-2 and I-3, the negative Z value increased in magnitude during the time interval; this was associated with the presence of occupied shoots in treatment subplot I-2 and unoccupied shoots in control subplot I-3. Therefore, table 6 presents six highly significant contrasts, two significant contrasts, and 16 contrasts of means that are not significantly different.

During the rainy season, a higher frequency of significant Z values among the subplot contrasts was recorded than during the dry or cool season (Tab.

TABLE 6. As in Table 4 except that the majority of the days in the time intervals occur in the cool season or before. Where two Z values are given on a single line, the first represents a comparison of the shoot lengths at the beginning of the interval and the second, the shoot lengths at the end of the interval. This was necessary because the earlier records were not kept on an individual plant basis and thus a standard deviation for the increment could not be calculated.

Sub-plot	Ants removed by	Time interval	Occupied Total		Length		Increment		Z values
			Begin	End	$\bar{X}_o$ (cm)	s.d.$_o$ (cm)	$\bar{X}_{inc}$ (cm)	s.d.$_{inc}$ (cm)	
C-1	R, T	5 Jan.-	0/20	2/20	0.00	0.0	16.25	13.8	—1.381
C-2	R		0/19	1/19	0.00	0.0	15.05	13.4	—1.086
C-3	C	14 Mar.	0/31	1/31	0.00	0.0	10.67	14.5	
E-1	R	18 Nov.-	0/29	0/29	0.00	0.0	3.31	3.9	2.220*
E-2	R		0/24	0/24	0.00	0.0	5.25	5.0	1.221
E-3	C	26 Nov.	21/21	11/21	0.00	0.0	7.95	9.0	
E-1	R	26 Nov.-	0/29	0/29	3.31	3.9	13.41	12.3	1.152
E-2	R		0/24	1/24	5.25	5.0	13.12	15.0	1.111
E-3	C	23 Mar.	11/21	10/21	7.95	9.0	18.71	18.3	
F-1	R	28 Oct.-	0/42	20/42	0.00	0.0	12.92	7.3	—0.187
F-2	C	28 Nov.	40/40	26/40	0.00	0.0	12.15	25.0	
F-1	R	28 Nov.-	20/42	11/42	12.92	7.3	9.08	9.5	—1.762
F-2	C	6 Jan.	26/40	27/40	12.15	25.0	5.45	9.2	
G-1	R	28 Oct.-	0/18	7/18	0.00	0.0	14.72	10.4	0.977
G-2	R		0/26	6/26	0.00	0.0	14.65	6.9	1.343
G-3	C	29 Nov.	24/24	16/24	0.00	0.0	17.70	8.9	
G-1	R	29 Nov.-	7/18	2/18	14.72	10.4	—3.56	13.9	3.688**
G-2	R		6/26	10/26	14.65	6.9	8.65	10.7	0.930
G-3	C	6 Jan.	16/24	15/24	17.70	8.9	11.71	12.4	
H-1	R, P,T	17 Oct.-	0/48	16/48	0.00	0.0	8.14	8.7	6.745**
H-2	R, P		0/69	18/69	0.00	0.0	12.47	8.6	4.746**
H-3	C	19 Nov.	61/61	61/61	0.00	0.0	20.35	10.2	
H-1	R, P, T	19 Nov.-	16/48	0/46	8.14	8.7	7.57	X	6.745** 8.850**
H-2	R, P		18/69	3/69	12.47	8.6	11.24	X	4.746** 6.015**
H-3	C	26 Dec.	61/61	48/68	20.35	10.2	22.25	X	
H-1	R, P, T	26 Dec.	0/46	0/43	15.34	13.4	—0.37	X	8.850** 8.949**
H-2	R, P		3/69	0/66	23.71	16.7	0.41	X	6.015** 6.111**
H-3	C	11 Mar.	48/68	65/72	42.60	19.9	1.20	X	
I-1	R	18 Oct.-	0/38	0/38	0.00	0.0	11.89	10.6	—1.283
I-2	R		0/31	0/32	0.00	0.0	9.43	6.4	—0.197
I-3	C	20 Nov.	39/39	13/37	0.00	0.0	9.08	8.3	
I-1	R	20 Nov.-	0/38	3/38	11.89	10.6	—1.68	X	—1.283 2.066*
I-2	R		0/32	0/32	9.43	6.4	8.21	X	—0.197 —0.225
I-3	C	26 Dec.	13/37	3/39	9.08	8.3	7.38	X	
I-1	R	26 Dec.-	3/38	12/38	10.10	16.7	2.53	13.6	0.782
I-2	R		0/32	0/32	17.09	14.5	—3.25	6.0	2.766**
I-3	C	13 Mar.	3/39	33/39	16.30	15.7	5.41	18.4	

14). This was due to several major factors. The treatment subplots in plots A and B were established in such a manner that only a low incidence of shoots remained occupied in spite of the treatments. Occupied shoots in all control subplots had sufficient water and insolation for high growth rates, which thereby accentuated the differences between them and the unoccupied shoots in the treatment subplots. Phytophagous insects were much more abundant during the rainy season than during any part of the preceding nine months, and their damage to the unoccupied shoots was much more severe. In the control subplots, a number of the colonies moved out into nearby shoots to establish auxiliary-units, and thereby occupied a number of shoots that were unoccupied or lightly occupied during part or all of the preceding nine months. This also increased the variation within the treatment subplots because the ants sometimes moved into the treatment subplots. In all of the treatment subplots except B-1 and A-1, many of the stumps that had been unoccupied for 4-9 months were dead and had no height increment during the rainy season. They produced a negative increment when they died.

During the dry season, cool season, and period before the cool season, the lower frequency of significant Z values among the subplots was for the most part associated with 1) lowered potential replacement rates of shoot tips, 2) lowered incidence of phytophagous insects, 3) less thorough and intensive occupation of auxiliary-shoots in the control subplots, 4) the dominant role of *Coxina hadenoides* as a defoliator that is relatively insensitive to attack by *Pseudomyrmex ferruginea,* 5) the ability of severely defoliated unoccupied suckers, and associated stumps, to live for 1-6 months and continue to produce occasional new shoots, and 6) the lack of shade from the surrounding leafless vegetation in the dry season so that slow growing shoots were not shaded.

With the exception of the period 26 Dec.-11 Mar. (for the most part during the cool season), plot H showed the highest and most consistent Z values throughout the year. If plot A and B had been established at the same time as plot H, it is very likely that they would have shown the same high Z values. Two plots, C and D never showed significant differences in mean length increment when treated as entire subplots. This was associated most strongly with the small sample size and presence of large numbers of occupied shoots in the treatment subplots, and unoccupied shoots in the control subplots.

Subplot height increment records for existing shoots. In table 7, the height increments are recorded for 13 plots which contain 26 subplots. The shoots are all shoots that were in existence before the beginning of the experiment. The height increment is that accrued for the most part during the rainy season; plots U and V showed little height increment during the cool and dry seasons. In the treatment subplots in plots K, Q, L, and P, thorn clipping was used to remove the ant colony. In plots R, T, U, and V, parathion was used to remove the ant colonies and no applications were made after 9 Dec. 1963. In the remaining plots (J, M, N, and O), the fall spray applications were followed during the cool or dry season by thorn clipping to remove the colonies that had reinvaded the thorns.

Of the 13 treatment-control subplot contrasts presented in table 7, 11 are based on mapped subplots in which individual records were kept. Of these 11, seven have a highly significant difference in mean height increment, three have a positive but not significant Z value, and only one has a negative Z value but again not significant. In one unmapped plot (K), the Z value changed from a negative value to a highly significant value which indicates that there was a significant difference between the mean height increments over the interval. In the other unmapped plot (V) the highly significant Z value changed from 4.207** to 6.087** over the 10 month interval which indicates a possible significant height increment during this period.

Since only three shoots in subplot J-2 were occupied by the end of the rainy season, the low Z value from the contrast of J-1 with J-2 was expected. The shoots in plot R were heavily shaded and the treatment and control subplots contained nearly equal numbers of occupied shoots. A very large portion of the shoots in the treatment subplots T-1 and U-1 were reoccupied by auxiliary-units from outside of the subplots by beginning of the rainy season so that these treatment and control subplots constitute a poor contrast of unoccupied and occupied subplots. While six of the time intervals for the 13 contrasts include all or a portion of the dry season, the major portion of the growth in all of the plots in table 7 took place during the 1964 rainy season.

In table 8, the height increments are recorded for 11 of the 13 plots in table 7. These 11 plots contained 22 subplots. Of the seven mapped plots, two have a highly significant difference in mean height increment. The shoots in plot J were unoccupied during the interval. In plot M the growth of the treatment subplot was not inhibited due to a lack of phytophagous insects during the dry season, and the presence of small unanticipated colonies of *P. ferruginea* that had developed in situ before the thorns were clipped. In plot Q, the greater height increment in the treatment subplot was associated with the production of flowering branches and the lack of defoliating insects. The situation in plot R was the same as during the rainy season; there was shading and a high number of occupied shoots in the treatment subplot.

Of the four unmapped plots, K and O showed changes in Z values over the interval which indicate a significant difference in mean height increment between the treatment and control subplots. The lack of an indication of a significant difference in the mean height increment between the treatment and control subplots in plot N was associated with the usual agents that tend to equalize height increment rates in treatment and control subplots during the 8 months preceding the rainy season. The considerable decrease in the Z value for plot P from the beginning to the end of the interval was strongly

TABLE 7. As in Table 4 (rainy season) except that the values are height, and height increment instead of length and length increment. This is because these values are for the existing shoots, rather than for suckers from stumps cut during the treatment schedule.

Sub-plot	Ants removed by	Time interval	Occupied Total		Height		Increment		Z values
			Begin	End	$\bar{X}_o$ (cm)	s.d.$_o$ (cm)	$\bar{X}_{inc}$ (cm)	s.d.$_{inc}$ (cm)	
J-1	P, T	25 Apr.-	0/29	0/29	22.72	8.1	5.13	9.6	1.073
J-2	C	23 Jul.	0/38	3/38	24.76	7.3	7.89	11.4	
K-1	T	4 Apr.-	0/205	0/266	35.76	11.5	−2.09	X	−2.530 4.839**
K-2	C	1 Aug.	48/138	49/149	32.06	14.5	12.81	X	
L-1	T	26 May-	0/44	0/44	69.04	28.6	−2.23	17.3	3.853**
L-2	C	31 Jul.	28/52	38/52	85.03	32.3	13.07	21.6	
M-1	P, T	26 May-	0/79	0/79	116.75	61.4	−1.35	23.1	9.066**
M-2	C	31 Jul.	59/88	59/88	87.81	39.2	26.03	21.7	
N-1	P, T	3 Apr.-	0/81	0/81	100.92	37.2	4.47	10.8	11.477**
N-2	C	29 Jul.	43/56	53/56	93.76	42.7	80.22	48.6	
O-1	P, T	3 Apr.-	0/38	0/38	85.89	36.5	4.76	14.4	10.083**
O-2	C	29 Jul.	32/34	34/34	102.73	38.5	92.79	49.1	
P-1	T	24 Mar.-	7/61	0/61	111.40	34.3	−4.76	19.2	5.892**
P-2	C	2 Aug.	28/46	34/46	100.26	64.8	61.82	74.9	
Q-1	T	30 May-	0/149	0/149	101.96	46.1	−0.74	3.1	8.660**
Q-2	C	6 Aug.	80/128	90/128	118.29	40.8	52.63	53.6	
R-1	P	28 May-	14/42	14/42	116.02	112.5	−9.65	23.0	1.370
R-2	C	27 Jul.	11/48	12/48	58.91	73.4	−2.32	36.3	
S-1	P	6 May-	55/211	95/211	166.54	91.7	10.41	34.8	5.864**
S-2	C	4 Aug.	175/251	195/251	158.63	76.9	32.05	44.4	
T-1	P	8 May-	50/116	102/116	195.75	94.1	12.87	40.7	1.439
T-2	C	29 Jul.	78/104	90/104	201.79	94.9	20.30	35.8	
U-1	P	21 Jan.-	39/86	78/86	363.18	103.2	11.45	28.2	−1.073
U-2	C	5 Jul.	78/93	85/93	335.05	92.7	2.90	74.9	
V-1	P	8 Oct.-	0/170	133/187	250.44	128.9	11.88	X	4.207** 6.087**
V-2	C	14 Jul.	191/192	192/205	308.93	135.5	39.22	X	

associated with the lack of any kind of growth in the control subplot and the production of flowering branches as a reaction to insect damage in the treatment subplot.

In table 9, the height increments are recorded for eight of the 13 plots in table 7. These contained 16 subplots. The one mapped plot (J) does not show a significant difference in height increment; none of its shoots were occupied. Of the unmapped plots, only the contrasts of heights in plots N and O during October and November show an indication of a significant differ-

Table 8. As in Table 5 (dry season) except for the changes necessary to account for the fact that these are existing shoots rather than suckers from experimentally cut stumps.

Sub-plot	Ants removed by	Time interval	Occupied/Total Begin	Occupied/Total End	Height $\bar{X}_o$ (cm)	Height s.d.$_o$ (cm)	Increment $\bar{X}_{inc}$ (cm)	Increment s.d.$_{inc}$ (cm)	Z values
J-1	P, T	15 Jan.-	0/29	0/29	22.24	8.9	0.48	3.5	−1.010
J-2	C	25 Apr.	0/38	0/38	25.26	7.9	−0.50	4.5	
K-1	T	22 Dec.-	0/178	0/205	38.84	15.0	−3.06	X	−4.329 −2.530
K-2	C	4 Apr.	42/153	48/138	32.00	13.8	0.06	X	
L-1	T	18 Jan.-	0/44	0/44	65.00	26.3	4.04	29.2	3.131**
L-2	C	26 May	20/52	27/52	64.36	20.3	20.67	21.4	
M-1	P, T	18 Jan.-	6/79	0/79	96.60	34.3	20.15	44.0	0.933
M-2	C	26 May	59/88	59/88	61.78	25.6	26.03	37.2	
N-1	P, T	20 Dec.-	20/81	49/81	105.92	62.2	−5.00	X	−1.033 −1.015
N-2	C	3 Apr.	51/56	43/56	97.50	32.4	−3.74	X	
O-1	P, T	20 Dec.-	5/38	0/38	88.42	40.8	−2.53	X	−0.573 1.898*
O-2	C	3 Apr.	32/34	32/34	81.02	64.9	21.71	X	
P-1	T	28 Dec.-	0/86	8/61	102.13	38.4	9.27	X	0.424 −1.060
P-2	C	24 Mar.	26/47	28/46	105.74	50.9	−5.48	X	
Q-1	T	16 Mar.-	7/149	0/149	93.28	49.0	8.68	9.9	−1.216
Q-2	C	30 May	94/128	80/128	113.10	43.4	5.19	31.2	
R-1	P	9 Dec.-	18/42	14/42	121.83	100.1	−5.81	17.9	−1.960
R-2	C	28 May	3/48	11/48	73.54	70.8	−14.63	24.6	
S-1	P	11 Jan.-	22/211	55/211	164.62	107.9	−1.92	41.7	2.480**
S-2	C	6 May	131/251	175/251	149.71	90.2	8.92	52.1	
T-1	P	6 Jan.-	17/116	50/116	194.87	93.7	0.88	5.6	0.038
T-2	C	8 May	82/104	78/104	200.87	94.8	0.92	9.1	

ence in the mean height increment over the interval. It should be emphasized that the height increments in plots N and O that were presented in table 7 and 8 only represent the shoots in these plots that were taller than 50 cm on 3 Apr. 1964. The sudden burst of growth in subplot M-1 was very likely associated with parathion stimulation and possibly with insecticide mortality to the general defoliators in the plot. The lack of significant differences in the contrasts presented in table 9 was for the most part associated with the lack of growth among all shoots during this time of year, the presence of unoccupied shoots in control subplots, and the presence of occupied shoots in treatment subplots.

Height or length increments of occupied shoots contrasted to unoccupied shoots. In the mapped plots, it was possible to determine which shoots re-

TABLE 9. As in Table 6 (cool season) except for the changes necessary to account for the fact that these are existing shoots rather than suckers from experimentally cut stumps.

			Occupied Total		Height		Increment			
Sub-plot	Ants removed by	Time interval	Begin	End	$\bar{X}_o$ (cm)	s.d.$_o$ (cm)	$\bar{X}_{inc}$ (cm)	s.d.$_{inc}$ (cm)	Z values	
J-1	P, T	12 Dec.-	0/29	0/29	23.93	7.8	−1.69	3.4		1.357
J-2	C	15 Jan.	0/38	0/38	25.81	7.8	−0.55	3.4		
L-1	T	12 Dec.-	0/44	0/44	68.97	27.8	−3.97	X	−0.383	−0.131
L-2	C	18 Jan.	7/69	20/52	66.95	26.4	−2.59	X		
M-1	P, T	28 Oct.-	7/97	27/85	61.30	23.7	36.46	X	5.466**	−7.553
M-2	C	6 Dec.	7/72	54/101	85.68	31.9	−21.08	X		
M-1	P, T	6 Dec.	27/85	7/79	97.76	31.1	−1.16	X	−7.553	−7.361
M-2	C	18 Jan.	54/101	59/88	64.60	28.2	2.82	X		
N-1	P, T	12 Oct.-	?/157	32/368	54.75	33.1	−15.98	X	−3.517	1.202
N-2	C	14 Nov.	?/136	53/243	42.65	25.7	−1.15	X		
N-1	P, T	14 Nov.-	32/368	35/342	38.77	38.2	9.00	X	1.202	−1.187
N-2	C	20 Dec.	53/243	44/240	41.50	14.9	1.97	X		
O-1	P, T	12 Oct.-	?/83	8/146	39.60	33.2	−0.58	X	−0.905	0.664
O-2	C	14 Nov.	?/179	40/145	35.66	31.9	4.65	X		
O-1	P, T	14 Nov.	8/146	9/183	39.02	13.9	4.27	X	0.664	−0.577
O-2	C	20 Dec.	40/145	31/181	40.31	18.9	1.04	X		
S-1	P	28 Oct.-	?/149	22/211	179.52	128.8	−14.95	X	−1.636	−1.594
S-2	C	11 Jan.	?/226	131/251	160.37	74.7	−10.66	X		
T-1	P	25 Oct.-	0/93	17/116	194.05	90.2	0.82	X	1.273	0.472
T-2	C	6 Jan.	93/94	82/104	211.11	91.9	−10.24	X		
U-1	P	28 Oct.-	?/99	39/86	356.36	105.6	6.82	X	−1.162	−1.913
U-2	C	21 Jan.	?/98	78/93	340.20	89.2	−5.15	X		

mained occupied and unoccupied for one or more intervals. By selecting the continuously occupied and the continuously unoccupied shoots from the entire plot (i.e., from both the treatment and control subplots), it was possible to remove a large part of the variation in length and height increments associated with the presence of occupied shoots in treatment plots, and unoccupied shoots in control plots. This selection also removes the variation associated with the abandonment of auxiliary-shoots during the dry season, and reinvasion of these shoots during the rainy season. The continuously occupied shoots contained queen-units and large auxiliary-units. The continuously unoccupied shoots were those treated shoots which were not reinvaded, or in which colonies had not yet developed in situ. There were a few shoots in the control subplots which were naturally unoccupied due to failure of a colony to develop in situ, abandonment of the shoot by the colony during the dry season, or destruction of the queen-unit in the neighboring treatment plot.

The samples of occupied shoots used in tables 10-13 were recorded as occupied or unoccupied consistently at each recording, from the earliest date listed for the particular plot, until the last date for the particular plot. For example, for a shoot to be used in any of the length increment means for plot G, it must have been recorded as occupied or unoccupied on 28 Oct., 29 Nov., 6 Jan., 24 Apr., and 6 Jul. For any given plot, as many intervals are presented in tables 10-13 as allows a reasonably large sample size; the more intervals, the fewer consistently occupied or unoccupied shoots that can be pooled from a single plot. The results based on this segregation of samples by ant presence or absence are presented under the following subtitles. They are also tabulated in table 14.

1. Length increment of suckers. Table 10 contains the length increment data for nine plots and 10 intervals during the 1964 rainy season. In the 10 contrasts between the mean length increments of occupied and unoccupied shoots, all of the Z values are highly significant. The 10 intervals yielded 329 length increments for occupied shoots and 433 length increments for unoccupied shoots. There is a total increase of 31,566 cm for the 329 occupied increments and a total increase of 1,487 cm for the 433 unoccupied increments. The maximum daily mean length increment was 2.079 cm and was recorded in plot I for 36 occupied shoots over 57 days. This value is very close to that of 2.50 cm per day that was recorded for nine occupied shoots from 10-28 Jul.; these nine shoots were known to be undamaged over the interval. The minimum daily mean length increment of −0.026 cm was also recorded in plot I; it was for 50 unoccupied shoots over a 57 day period.

In Table 10, the high increment rates of occupied shoots, in contrast to the low increment rates of unoccupied shoots, were definitely correlated with the lack of insect damage and shading of the shoot tips, both before and during the interval. The low increment rates were definitely correlated with shading and severe insect defoliation of the unoccupied shoots, both before and during the interval. Many of the shoots that had been unoccupied for two or more months were dead.

Table 11 contains the length increment data for seven plots and 10 intervals during the nine months preceding the 1964 rainy season. Of the 10 contrasts, nine of the Z values are highly significant. The 10 intervals yield 261 length increments for occupied shoots and 379 length increments for unoccupied shoots. There is a total increase of 10,211 cm for the 261 occupied increments and a total increase of 1,880 cm for the 379 unoccupied increments. The maximum mean daily length increment of 1.54 cm was recorded in plot E for 21 occupied shoots over 79 days. The minimum daily length increment of −0.0146 cm was recorded in plot F for 26 unoccupied shoots over a 91 day

TABLE 10. Length increment data for suckers from stumps, treated as occupied and unoccupied groups rather than by subplots as in Table 4. Time interval during the rainy season. Terminology as in Table 4.

				Length		Increment		
Plot	Time interval	Occupation	Number of shoots	$\bar{X}_0$ (cm)	s.d.$_0$ (cm)	$\bar{X}_{inc}$ (cm)	s.d.$_{inc}$ (cm)	Z values
A	25 May- 16 Jun.	unoccupied occupied	41 25	0.00 0.00	0.0 0.0	5.78 33.00	4.8 17.1	7.777**
A	16 Jun.- 3 Aug.	unoccupied occupied	41 25	5.78 33.00	4.8 17.1	11.78 77.28	9.4 58.3	8.397**
B	23 May- 17 Jun.	unoccupied occupied	36 42	4.13 16.52	7.1 10.0	22.14 60.76	21.6 15.3	8.981**
B	17 Jun.- 7 Aug.	unoccupied occupied	36 42	26.27 77.28	6.4 14.2	7.24 117.28	11.7 19.4	14.321**
C	27 May- 6 Aug.	unoccupied occupied	47 16	25.31 62.80	28.5 51.9	0.68 122.25	20.3 52.4	9.072**
D	25 May- 28 Jul.	unoccupied occupied	13 22	21.76 52.18	24.3 49.3	−0.61 56.40	21.5 43.1	5.230**
F	24 Apr.- 6 Jul.	unoccupied occupied	26 26	18.03 46.23	13.9 11.8	4.69 68.91	10.8 35.3	8.870**
G	24 Apr.- 6 Jul.	unoccupied occupied	25 15	17.15 42.46	14.1 15.0	5.50 83.66	11.8 27.5	10.449**
H	10 Jun.- 5 Aug.	unoccupied occupied	79 59	13.50 96.05	15.5 41.1	−0.97 114.62	11.2 64.2	13.679**
I	10 Jun.- 6 Aug.	unoccupied occupied	50 36	5.36 80.44	10.2 40.2	−1.30 118.55	5.1 34.3	20.807**

period. The single contrast with a very low Z value (plot G) is from a plot in which there was a consistent removal of shoot tips by *Coxina hadenoides* from both occupied and unoccupied shoots.

The length increments recorded for occupied shoots in the cool and dry season (Tab. 11) were lower than those recorded for occupied shoots in the rainy season (Tab. 10). During the cool and dry season there was a lowered replacement rate of shoot tips so that when a shoot tip was destroyed (e.g., by *Coxina hadenoides*), more time was required for a positive height increment to begin. During the cool season, the nights were often cold enough so that shoots that were recorded as occupied during the day did not have workers on their outer surface at night. During the dry season, the number of workers active on the surface of the shoot was generally reduced even at high temperatures; occasionally an insect could eat all or part of a shoot tip without coming in contact with an aggressive worker.

TABLE 11. As in table 10 (rainy season) except time interval during the dry season.

			Number	Length		Increment		
Plot	Time interval	Occupation	of shoots	$\bar{X}_o$ (cm)	s.d.$_o$ (cm)	$\bar{X}_{inc}$ (cm)	s.d.$_{inc}$ (cm)	Z values
C	17 Mar.-	unoccupied	47	15.19	12.5	10.12	19.8	4.181**
	27 May	occupied	16	11.37	18.7	51.43	37.7	
D	10 Dec.-	unoccupied	13	0.00	0.0	21.76	24.3	2.433**
	25 May	occupied	22	0.00	0.0	52.18	49.3	
E	23 Mar.-	unoccupied	39	14.87	12.4	17.71	26.3	13.336**
	10 Jun.	occupied	21	26.66	22.7	122.00	30.2	
F	6 Jan.-	unoccupied	26	17.70	11.3	−0.33	9.5	4.298**
	24 Apr.	occupied	26	27.00	12.8	19.23	21.2	
G	28 Oct.-	unoccupied	25	0.00	0.0	11.80	5.5	4.077**
	29 Nov.	occupied	15	0.00	0.0	21.26	7.9	
G	29 Nov.-	unoccupied	25	11.80	5.5	−0.11	8.1	5.323**
	6 Jan.	occupied	15	21.26	7.9	15.54	9.5	
G	6 Jan.-	unoccupied	25	11.69	10.2	5.46	10.3	0.059
	24 Apr.	occupied	15	36.80	13.6	5.66	10.2	
H	11 Mar.-	unoccupied	79	14.83	18.1	−1.33	15.1	10.435**
	10 Jun.	occupied	59	49.69	18.1	46.36	32.6	
I	13 Mar.-	unoccupied	50	4.34	3.1	−0.30	3.0	8.836**
	18 Apr.	occupied	36	30.25	21.0	17.61	12.2	
I	18 Apr.-	unoccupied	50	4.04	7.3	1.22	8.2	6.272**
	10 Jun.	occupied	36	47.86	30.3	32.58	29.2	

The length increments recorded for unoccupied shoots during the dry season (Tab. 11) are higher than those recorded for unoccupied shoots during the rainy season (Tab. 10). During the cool and dry season there was a severe reduction in general insect density in the plots and associated with this, an unoccupied shoot was occasionally recorded as having an intact terminal shoot tip for as long as a month. Since it required 1-9 months for an unoccupied shoot to sustain enough damage to kill it, many of the unoccupied shoots included in table 11 were not dead. Many more of them were dead during the interval in the rainy season (Tab. 10). These dead shoots are included because they are dead owing to the lack of ants to keep them alive.

Both the experimental plots and observations of suckers from naturally occurring stumps indicated that the data presented in tables 10-11 are representative of length increment rates in both naturally occurring and man-made disturbance sites in the area between Temascal and La Granja. At the present, at least 99 per cent of the shoots that reach maturity in this area are occupied sucker shoots from stumps that were cut or burned. At any particular season, the differences between the increment rates of occupied and unoccupied shoots are due to the relatively severe insect damage to unoccupied shoots, and the inability of unoccupied shoots to maintain an emergent position in the general vegetation canopy.

2. Height increments of existing shoots. Table 12 contains the height increment data for occupied and unoccupied shoots for seven plots and seven intervals during the 1964 rainy season. In all of the seven contrasts, the Z values are highly significant. The seven intervals yielded 413 height increments for the occupied shoots and 716 height increments for the unoccupied shoots. There was a total increase of 38,056 cm for the 413 occupied increments and —1,324 cm for the 716 unoccupied increments. The maximum daily mean height increment was 1.58 cm and was recorded in plots N and O combined for 95 occupied shoots over a period of 119 days. The minimum daily mean height increment was —0.26 cm and was recorded in plot R for 57 unoccupied shoots over a period of 59 days.

The variation in height increment of occupied shoots between plots, during the rainy season, was primarily due to local differences in abundance of those phytophagous insects that can feed in the presence of *P. ferruginea.*

Table 13 contains the height increment data for occupied and unoccupied shoots in four plots and four intervals during the 1964 dry season. In three of the four contrasts, the Z values are highly significant. The fourth contrast (Q) does not have a significant Z value. The four intervals yielded 267 height increments for the occupied shoots and 466 height increments for the unoccupied shoots. There was a total increase of 3,634 cm for the 267 occupied shoot increments and 1,621 cm for the 466 unoccupied shoot increments. The maximum mean daily height increment was 0.29 cm and was recorded in plot M for 44 shoots over a period of 128 days. The minimum daily mean height increment was —0.05 cm and was recorded in plot S for 181 shoots over a period of 114 days.

The variation in height increment of occupied shoots during the dry season was primarily due to local differences in abundance of *Coxina hadenoides* (Q), and increasing dry season dormancy with increasing age of the shoot (S). In addition to the above two major factors, the variation in height increment of unoccupied shoots during the dry season was due to the production of short vertical flowering branches (Q and P) and cutting of the shorter shoots by *Sigmodon hispidus* (S).

Discussion. It is evident from the data presented in tables 4-13 that the presence of the workers of a colony of *Pseudomyrmex ferruginea* on a shoot of *Acacia cornigera* has an effect on the length increment of the shoot (Fig. 53-59). That the presence or absence of this effect, and its magnitude, varies with the time of year and the size of the shoot, can be clearly seen in table 14. The time of year affects the abundance of phytophagous insects, the physiological growth rates of the shoot, and the shading effects of the sur-

TABLE 12. Height increment data for existing shoots treated as occupied and unoccupied groups rather than by subplots as in Table 7. Time interval during the rainy season.

				Height		Increment		
Plot	Time interval	Occupation	Number of shoots	$\bar{X}_o$ (cm)	s.d.$_o$ (cm)	$\bar{X}_{inc}$ (cm)	s.d.$_{inc}$ (cm)	Z values
L	26 May- 31 Jul.	unoccupied	49	68.27	27.1	—2.30	15.5	3.616**
		occupied	12	103.66	33.7	20.16	20.1	
M	26 May- 31 Jul.	unoccupied	77	107.94	61.2	—0.38	14.6	8.990**
		occupied	44	109.06	17.4	45.11	40.0	
N, O	3 Apr.- 31 Jul.	unoccupied	122	95.98	37.1	5.47	15.1	28.534**
		occupied	95	100.68	43.5	188.66	61.2	
P	24 Mar.- 2 Aug.	unoccupied	71	103.91	34.4	—9.78	24.9	19.344**
		occupied	34	113.02	72.1	172.64	52.2	
Q	30 May- 6 Aug.	unoccupied	159	96.87	47.2	—1.10	11.2	15.627**
		occupied	68	141.45	23.4	79.85	42.1	
R	28 May- 26 Jul.	unoccupied	57	58.82	88.8	—15.68	53.4	3.250**
		occupied	17	159.76	103.9	23.00	39.2	
S	5 May- 3 Aug.	unoccupied	181	122.99	78.9	—0.48	24.1	11.590**
		occupied	143	200.36	78.8	43.47	43.2	

TABLE 13. As in Table 12 (rainy season) except time interval during the dry season.

				Height		Increment		
Plot	Time interval	Occupation	Number of shoots	$\bar{X}_o$ (cm)	s.d.$_o$ (cm)	$\bar{X}_{inc}$ (cm)	s.d.$_{inc}$ (cm)	Z values
L	18 Jan.- 26 May	unoccupied	49	62.90	24.8	5.37	28.0	3.534**
		occupied	12	74.50	24.6	29.16	19.3	
M	18 Jan.- 26 May	unoccupied	77	93.16	35.8	14.78	23.2	5.753**
		occupied	44	72.36	21.6	36.70	18.2	
P	19 Mar.- 30 May	unoccupied	159	89.27	29.5	7.60	31.0	0.437
		occupied	68	132.48	41.6	8.97	16.0	
S	11 Jan.- 5 May	unoccupied	181	128.45	70.2	—5.46	47.2	3.193**
		occupied	143	192.95	74.4	7.41	11.2	

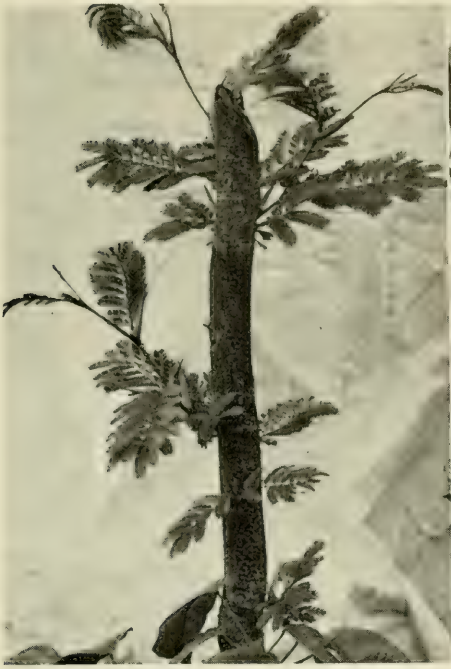


Fig. 53 (left). A 65 cm tall cut stump of *Acacia cornigera* in control subplot H-3. The regenerating branches are occupied by *P. ferruginea* and the stump has been cut for about 35 days. There are three number 4 shoot tips on the stump. This is a representative shoot. Photo late November 1963.

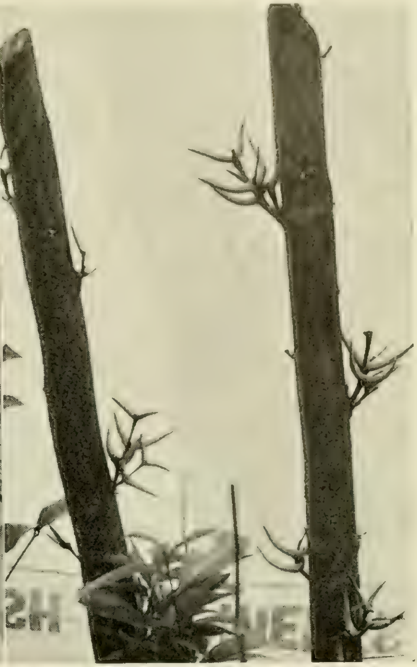


Fig. 54 (right). Two 65 cm tall cut stumps of *Acacia cornigera* in treatment subplot H-1. The regenerating branches are unoccupied and the stumps have been cut for about 35 days. This stump would receive a rating of 1.5 because it is still alive. The unoccupied foliage was eaten by adult tettigoniid grasshoppers. These are representative shoots. Photo same date as in Fig. 53.

rounding vegetation. In those places where *Sigmodon hispidus* was present, the season influenced the amount of damage done by this rodent since it fed on *Acacia cornigera* for the most part only during the dry season. The size of the shoot affected its ability to withstand both insect and rodent damage. The size of the shoot also affected its responsiveness to changes in weather (e.g., from the dry season to the rainy season) which in turn affected the ants' opportunity to influence the shoots' height increment.

The lower Z values in the subplot contrasts were for the most part associated with the presence of unoccupied shoots in the control subplots, and of occupied shoots in the treatment subplots. These shoots were present because of the gradual reinvasion of the shoots in the treatment subplots by large colonies, the development of colonies in situ in the treatment subplots, and the partial or total abandonment of auxiliary-shoots in the control subplots during the cool and dry seasons. When groups of consistently occupied or unoccu-

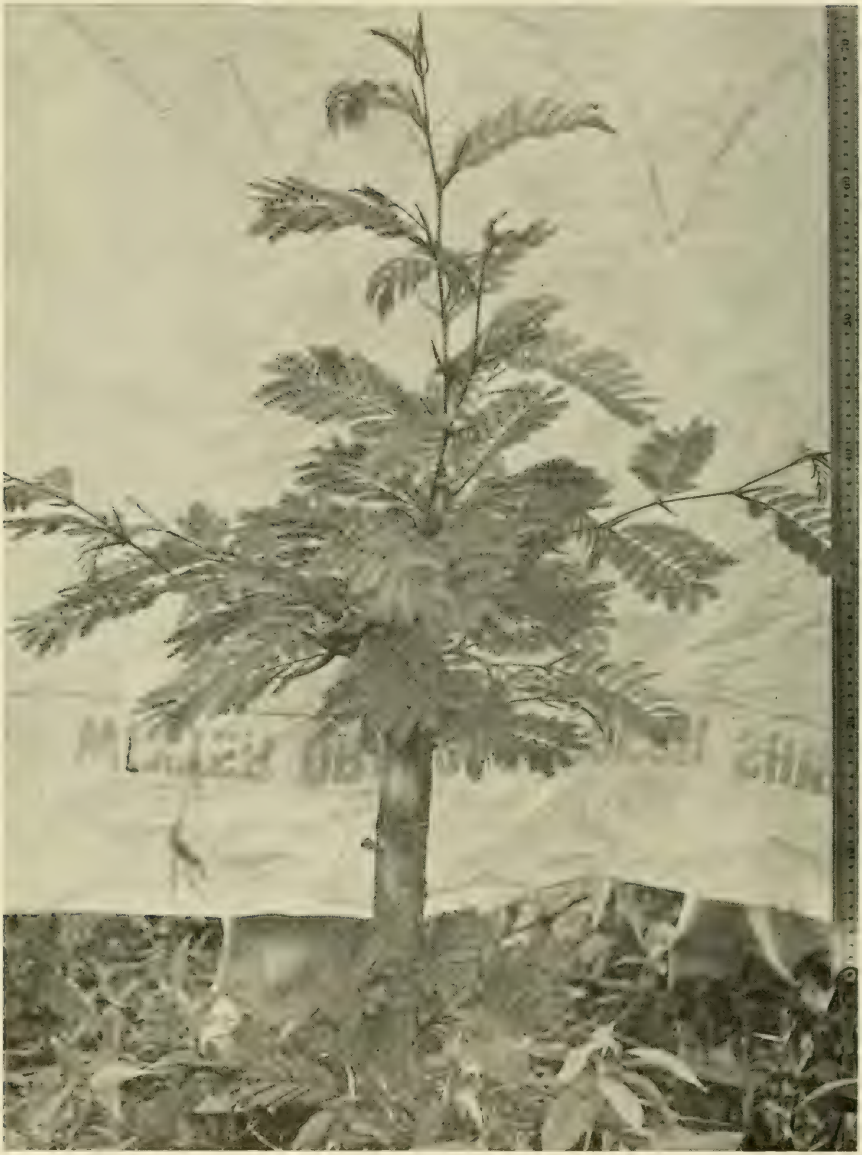


FIG. 55. A representative sucker shoot from a cut stump of *Acacia cornigera* in control subplot H-3. The shoot is occupied and has a number four shoot tip. The stump was cut on 17 Oct. 1963. Photo 21 Dec. 1963. This is the same stump as the one in Fig. 57.

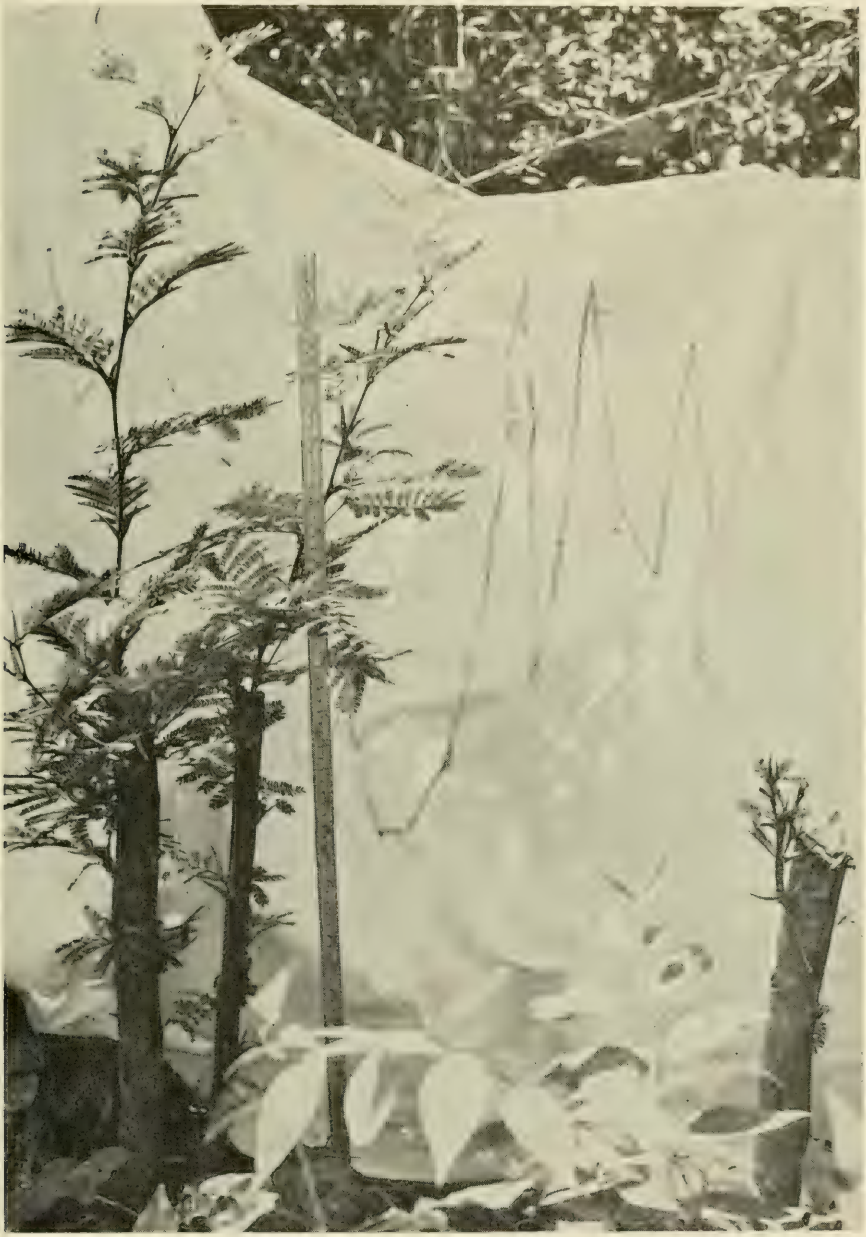


FIG. 56. Three stumps of *Acacia cornigera* in treatment subplot I-2. The two shoots on the left were reinvaded by auxiliary-units from shoots outside of the plot. The shoots on the right remained unoccupied until the photograph was taken. Shortly after this photograph, it became occupied by a unit from the shoots on the left; by July 1964 it was over 200 cm tall. Most of the unoccupied shoots in plot I continued to look like the one on the right throughout the entire experiment. Photo early January 1964.

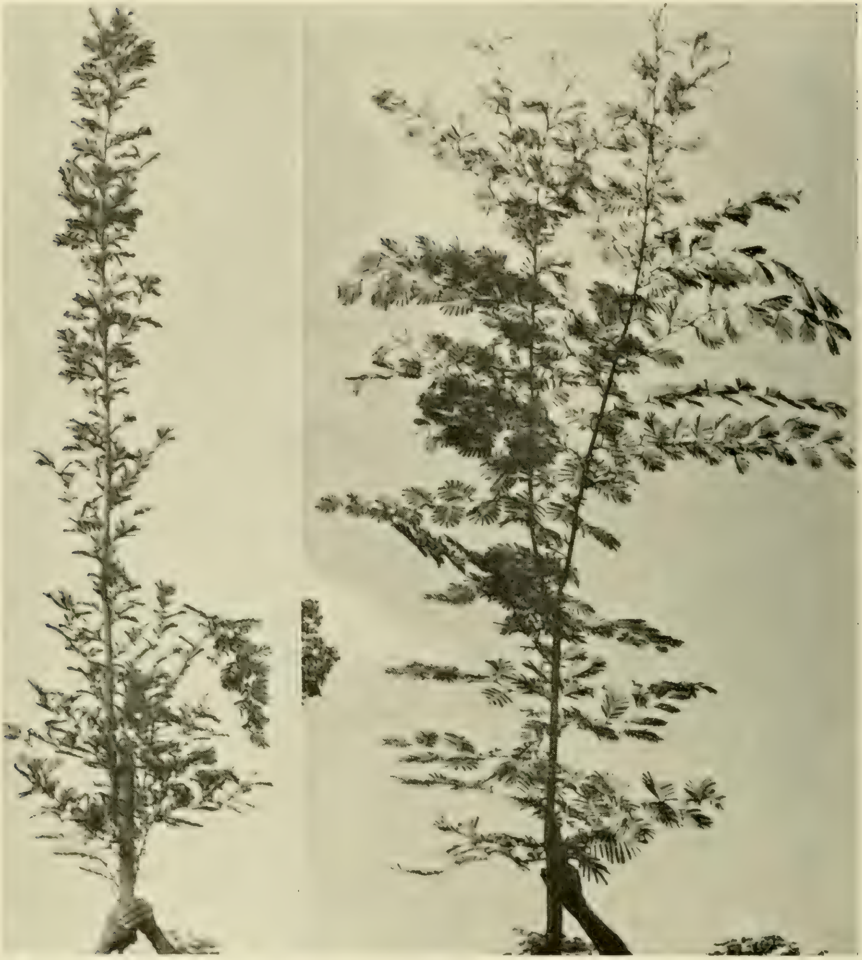


Fig. 57 (left). The same shoot as the one shown in Fig. 55. A heavily occupied shoot in control subplot H-3, it was 305 cm tall at the time the photograph was taken. Note the slender pole-like life form, despite the fact that the surrounding vegetation was only about 70 cm tall. This shoot is representative of most shoots in control subplot H-1, I-3, E-3, and F-2, although many were more spreading as in Figure 58. The stump was cut on 17 Oct. 1963. Photo 5 Aug. 1964.

Fig. 58 (right). A heavily occupied shoot in control subplot E-3. The shoot was 365 cm tall when the photograph was taken on 6 Aug. 1964. This shoot is representative of occupied shoots regenerating from large stumps in the control subplots. This shoot was cut on 18 Nov. 1963.

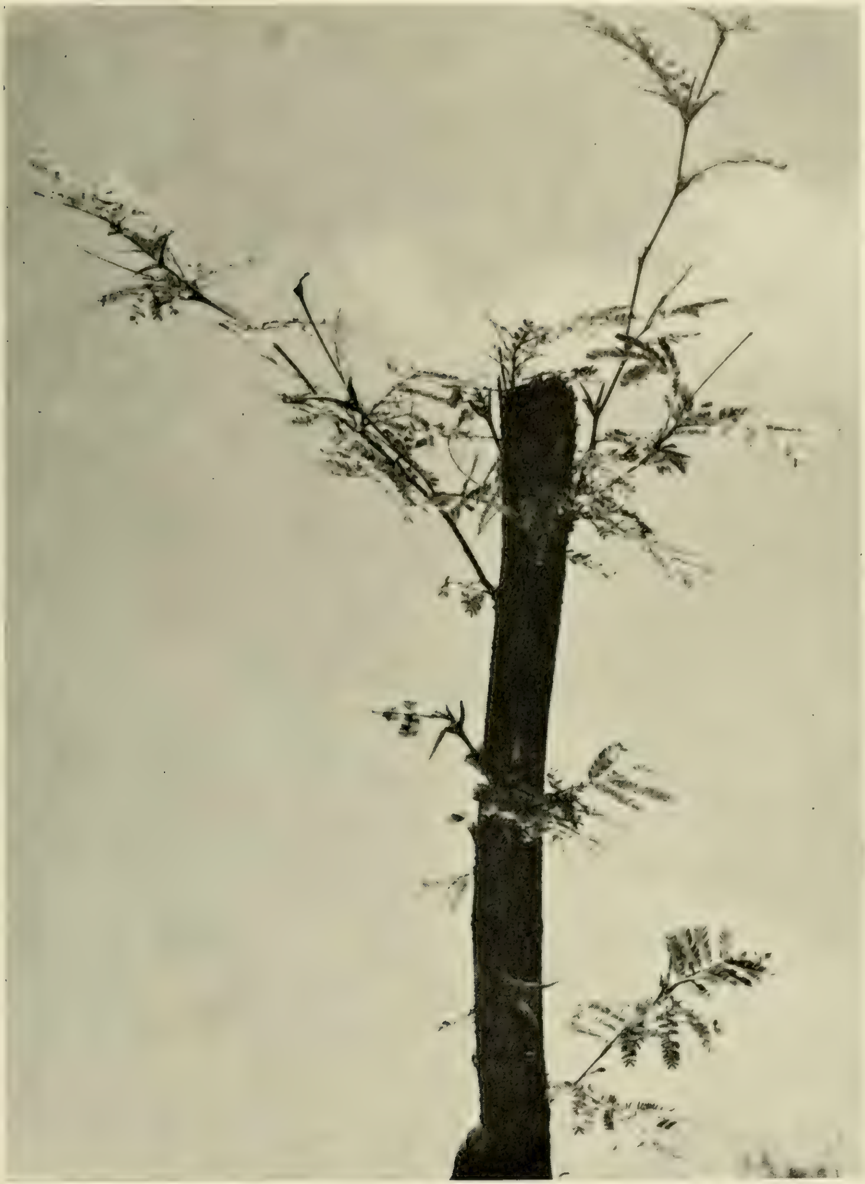


FIG. 59. A representative unoccupied shoot in treatment subplot E-3. The stump is the same size as the stumps of the shoots in Fig. 57 and 58. This shoot would be rated as a number 2.5. All damage is phytophagous insect damage. It is representative of the unoccupied shoots in treatment subplots H-1, H-2, C-1, C-2, E-1, E-2, F-1, G-1, G-2, I-1, and I-2. The stump was cut on 18 Nov. 1963. Photo 6 Aug. 1964.

TABLE 14. The distribution of significant Z values among contrasts of length or height increment of *Acacia cornigera* made at different times of the year. Note that the highest frequencies of Z values are associated with recordings made during the rainy season of subplots, or groups, of suckers from stumps. Those contrasts where the standard deviation of the increment was not available are omitted from this table.

Table	Time of year	Number of contrasts	Number highly significant contrasts	Number significant contrasts	Number not significant contrasts	Type of shoots
(treated as subplots)						
4	rainy	17	11	1	5	suckers
5	dry	16	6	2	8	suckers
6	cool & before	18	4	1	13	suckers
7	rainy	11	7	0	4	existing shoots
8	dry	7	2	0	5	existing shoots
9	cool	1	0	0	1	existing shoots
(treated as groups of shoots)						
10	rainy	10	10	0	0	suckers
11	dry	10	9	0	1	suckers
12	rainy	7	7	0	0	existing shoots
13	dry	4	3	0	1	existing shoots

pied shoots were compared (Tab. 10-13), these sources of variation were excluded. A relatively important source of variation in height increment among occupied shoots that was not removed by grouping occupied and unoccupied shoots was that associated with the size of the colony; the larger the number of workers active outside of the thorns, the larger the number of intact shoot tips on the shoot. A contrast between consistently occupied or unoccupied shoots is primarily one between healthy undamaged shoots that are that way because they contain a large worker force, and damaged and dying shoots that are that way because they have no worker force.

During the rainy season, the high density of phytophagous insects, and the high growth rate of undamaged shoots, tends to emphasize the differences between the occupied and unoccupied shoots. Better than 90 percent of the height increment of *Acacia cornigera* occurs during the five months between 1 Jun. and 1 Dec. It is likewise at this time when the highest densities of *Pseudomyrmex ferruginea* on occupied shoots are recorded. Superficial observation of populations of *A. cornigera* in other parts of the study area indicates that the length and height increment parameters presented in tables 4-13 are representative of those throughout the study area, provided that the shoots are of comparable size and growing in similar plant communities.

Condition of the shoot. Significance. The mean condition of the shoots in a subplot, or in a group of occupied or unoccupied shoots, is a measure of the amount of growth that is taking place at the time. For the shoot to produce new leaves and branches, it has to maintain undamaged shoot tips for a certain period. Even when the shoot tips are damaged, and few new leaves are being produced (during the cool and dry seasons), the condition is a measure of the amount of damage sustained by the mature leaves and branches. In treatment subplots, and among groups of unoccupied shoots, the condition of the shoots serves as a relatively instantaneous measure of the activity of insects that feed on *A. cornigera.* Since condition records do not cover an interval, they can be more readily segregated into those that are recorded during the various seasons. In control plots and groups of occupied shoots, condition records serve as a measure of the degree of occupation of the shoots, and of the density of insects that are relatively unaffected by the presence of *P. ferruginea.* The condition of the shoots is also a cumulative measure of the impact of phytophagous insects on the shoots. It often takes a month or more for a shoot to be sufficiently damaged to receive a condition rating below 3.

Height increment and condition are not independent variables. Height increment is a cumulative function of the condition of the uppermost shoot tip of the shoot over an interval of time. However, the condition of the uppermost shoot tip has a major influence only on the value of the condition rating for values 3, 3.5, and 4. The rating of a shoot could decrease from 3-1 without a change in shoot height. When the shoot is dying, and the condition rating falls below 2, a negative height increment is often recorded because of the loss of branches.

The condition of the unoccupied shoots on a site is often a very sensitive indicator of rapid changes in the density of phytophagous insects that attack *A. cornigera.* It was often the case in Oct. and Nov. 1963 that within five days after removing the ant colony from a shoot with parathion, the previously undamaged shoot tips were all eaten by Coleoptera, Orthoptera, and/or Lepidoptera. At the relatively sudden onset of the cool season about 1 Dec. 1963, there was a sharp reduction in the number of intact shoot tips on shoots that were occupied during the day. At night the temperatures were so low that the shoots were unoccupied, and adult tettigoniid grasshoppers and the larvae of *Coxina hadenoides* fed unhindered on the shoot tips. When the first rains fell at the beginning of the 1964 rainy season (20-23 May) there was a sudden hatch of *Diplotaxis denigrata.* These nocturnal feeders destroyed almost every previously intact shoot tip on unoccupied shoots in plots L and M within three days.

Subplot records of condition for suckers from stumps. The condition records for nine plots and 17 sets of independent recordings from sucker growth during the rainy season are given in table 15. There are 28 possible contrasts between control and treatment subplots. Of these 28 contrasts, 17 have a highly significant value, four have a significant Z value, and seven do not have a significant Z value. The low value in plot B on 17 June was most strongly associated with a very high density of *Coxina hadenoides* which lowered the condition value for the control subplot, and a low density of those insects which feed on unoccupied *Acacia cornigera*. This latter factor was apparently associated with the relatively barren aspect of the plant community in plot B. In plot D and F, the low Z values were associated with high numbers of occupied shoots in the treatment subplots. The negative values in plot C were associated with the fact that by the beginning of the rainy season almost every unoccupied shoot in control subplot C-3 was dead or nearly dead and thus had a condition rating of 0-1.

The condition records for six plots and seven sets of independent recordings during the dry season are given in table 14. There are 13 possible contrasts and of these, seven have a highly significant Z value, one has a significant Z value, and five do not have a significant Z value. The low Z values in all contrasts in table 16 are primarily associated with the general lack of insects that feed on unoccupied shoots of *A. cornigera* during the dry season. In plot F and G, the situation was further complicated by the presence of occupied shoots in the control subplots. Plot C is particularly instructive. The shoots were cut on 5 Jan. 1964 and the canopies removed from the stumps in the control as well as in the treatment subplot. The canopies were not placed on the stumps in the control subplot until 14 Mar. 1964. Therefore, the control subplot was essentially unoccupied during the period preceding the record of condition on 14 Mar.

The condition records for four plots and four sets of independent recordings during the cool season are given in table 17. There are seven possible contrasts and of these, four have a highly significant Z value while three do not have significant Z values. The three low Z values are associated with the presence of occupied shoots in treatment plots and a reduction of phytophagous insect density during the cool season. Plot I shows the effect of previous occupation on condition values. Nearly all of the occupied shoots in control subplot I-3 were occupied as small auxiliary-units. When the weather turned cold about 1 Dec., most of them were merged with the queen-unit and this left only three occupied shoots out of 39. Since the weather was cold there was little damage that occurred immediately to the vacated shoots. The shoots in the two treatment subplots had low condition values because of the cumulative effect of a month of insect damage in November.

The condition records of three plots and three sets of independent recordings during the end of the rainy season and shortly before the cool season are given in table 18. Of the five possible contrasts between control and treatment subplots, one has a highly significant Z value, one has a significant Z value,

TABLE 15. The condition values of the sucker shoots for which length increments were recorded and treated by subplots (Table 4-6). All recordings made during the rainy season.

Sub-plot	Date	Number shoots occupied/total	$\overline{X}$ Condition	s.d.^{2}	Z value
A-1	16 Jun.	0/42	3.309	0.731	3.514**
A-2	16 Jun.	26/29	3.896	0.310	
A-1	3 Aug.	0/42	2.654	0.628	7.623**
A-2	3 Aug.	29/29	3.706	0.116	
B-1	23 May	3/53	2.839	1.372	6.236**
B-2	23 May	41/47	3.893	0.375	
B-1	17 Jun.	7/53	3.245	0.871	2.187*
B-2	17 Jun.	44/47	3.595	0.441	
B-1	7 Aug.	19/53	2.641	1.639	5.570**
B-2	7 Aug.	45/47	3.744	0.626	
C-1	27 May	2/20	3.100	0.384	—2.126
C-2	27 May	2/19	3.289	0.592	—2.645
C-3	27 May	13/31	2.564	1.379	
C-1	6 Aug.	6/20	2.150	1.488	—0.788
C-2	6 Aug.	5/19	2.184	1.811	—0.789
C-3	6 Aug.	14/31	1.838	2.998	
D-1	25 May	3/9	2.666	1.187	1.320
D-2	25 May	6/12	2.833	0.879	1.128
D-3	25 May	15/19	3.210	0.731	
D-1	28 Jul.	3/9	2.444	1.528	1.797*
D-2	28 Jul.	7/12	2.291	1.657	2.294*
D-3	28 Jul.	16/19	3.289	0.981	
E-1	10 Jun.	4/29	3.120	0.529	5.818**
E-2	10 Jun.	2/24	2.479	1.249	6.321**
E-3	10 Jun.	21/21	3.952	0.048	
E-1	7 Aug.	6/29	2.310	1.257	7.971**
E-2	7 Aug.	4/24	1.333	1.666	9.973**
E-3	7 Aug.	21/21	3.976	0.012	
F-1	6 Jul.	26/42	2.726	0.966	1.900*
F-2	6 Jul.	29/40	3.087	0.524	
G-1	6 Jul.	6/18	2.166	0.647	4.213**
G-2	6 Jul.	9/26	3.019	0.350	1.236
G-3	6 Jul.	19/24	3.291	0.846	
H-1	10 Jun.	0/43	1.988	1.517	7.843**
H-2	10 Jun.	2/66	2.393	1.088	8.027**
H-3	10 Jun.	67/72	3.541	0.294	
H-1	5 Aug.	0/43	1.058	1.276	13.537**
H-2	5 Aug.	32/66	2.166	2.327	7.050**
H-3	5 Aug.	64/72	3.576	0.349	
I-1	10 Jun.	13/38	2.302	2.020	2.605**
I-2	10 Jun.	8/32	2.306	1.678	2.609**
I-3	10 Jun.	27/39	3.128	1.851	
I-1	5 Aug.	15/38	1.552	3.308	2.769**
I-2	5 Aug.	8/32	1.419	2.901	3.058**
I-3	5 Aug.	27/39	2.679	3.072	

TABLE 16. As in Table 15 (rainy season) except that the recordings were made during the dry season.

Sub-plot	Date	Number Shoots occupied/total	$\overline{X}$ Condition	s.d.^{2}	Z value
C-1	14 Mar.	2/20	2.550	1.260	—0.113
C-2	14 Mar.	1/19	2.947	0.636	—1.752
C-3	14 Mar.	1/31	2.516	0.917	
E-1	23 Mar.	0/29	2.948	1.113	2.049*
E-2	23 Mar.	0/24	2.729	0.716	3.197**
E-3	23 Mar.	11/21	3.442	0.417	
F-1	24 Apr.	19/42	3.238	0.746	1.383
F-2	24 Apr.	25/40	3.512	0.865	
G-1	24 Apr.	1/18	2.722	1.389	1.353
G-2	24 Apr.	5/26	3.423	0.254	—1.278
G-3	24 Apr.	10/24	3.166	0.732	
H-1	11 Mar.	0/43	2.139	1.039	5.902**
H-2	11 Mar.	0/66	2.750	0.294	4.038**
H-3	11 Mar.	65/72	3.166	0.671	
I-1	13 Mar.	12/38	1.907	3.106	3.265**
I-2	13 Mar.	0/32	1.859	2.181	3.586**
I-3	13 Mar.	33/39	3.089	1.919	
I-1	18 Apr.	14/38	2.105	3.488	3.181**
I-2	18 Apr.	7/32	1.859	2.987	3.798**
I-3	18 Apr.	29/39	3.333	2.230	

TABLE 17. As in Table 15 (rainy season) except that the recordings were made during the cool season.

Sub-plot	Date	Number shoots occupied/total	$\overline{X}$ Condition	s.d.^{2}	Z value
F-1	6 Jan.	11/42	3.261	0.332	—1.800
F-2	6 Jan.	27/40	3.000	0.530	
G-1	6 Jan.	2/18	2.916	0.654	1.442
G-2	6 Jan.	10/26	3.269	0.204	—0.294
G-3	6 Jan.	15/24	3.229	0.260	
H-1	26 Dec.	0/46	2.902	1.118	4.109**
H-2	26 Dec.	3/69	1.934	0.678	13.357**
H-3	26 Dec.	48/68	3.617	0.418	
I-1	26 Dec.	3/38	2.684	1.681	3.521**
I-2	26 Dec.	0/32	2.781	1.321	3.180**
I-3	26 Dec.	3/39	3.487	0.309	

TABLE 18. As in Table 15 (rainy season) except that recordings made during the late end of the 1963 rainy season immediately before the cool season.

Sub-plot	Date	Number shoots occupied/total	$\bar{X}$ Condition	s.d.^{2}	Z value
E-1	26 Nov.	0/29	2.775	1.046	0.967
E-2	26 Nov.	0/24	3.062	0.767	0.030
E-3	26 Nov.	11/21	3.071	1.207	
F-1	28 Nov.	20/42	3.511	0.335	−1.739
F-2	28 Nov.	26/40	3.137	1.538	
G-1	29 Nov.	7/18	3.361	0.808	2.534**
G-2	29 Nov.	6/26	3.596	0.576	2.012**
G-3	29 Nov.	16/24	3.916	0.080	

and three do not have a significant Z value. The fact that all of the Z values are relatively low was very strongly associated with the fact that newly cut unoccupied stumps tend to continue to produce new shoots for a month or more despite the continued defoliation by insects. In addition, phytophagous insects were much less abundant than they were during the first three months of the rainy season, and control subplot E-3 and F-2 had a number of unoccupied shoots in them.

Plot A, B and H yielded highly significant Z values throughout their recordings. Plot C yielded no significant Z values. These two extremes were associated, in the first case, with treatment subplots which had relatively few occupied shoots, and in the second case, with a control subplot which had many unoccupied shoots in it.

Subplot records of condition for existing shoots. The condition records for 12 plots and 16 independent recordings during the rainy season are given in table 19. Of the 16 possible contrasts between the control and treatment subplots, 11 have a highly significant Z value, and five do not have a significant Z value. The low Z value in plot J was associated with the fact that the control plot only had three occupied shoots in it; these three shoots were the three tallest shoots in the plot, had intact shoot tips, and were emergent. The high condition value in plot Q-1 was the result of flowering branches produced in thorn axils in the upper part of the shoot; the low condition value in plot Q-2 was the result of a general slowness in this plot to initiate vertically lengthening branches at the end of the dry season. The low Z values recorded for plot R were due to the large number of occupied shoots in the treatment subplot; the low condition values for both subplots were due to the heavy shade in plot R. Heavily shaded shoots were generally very slow to replace damaged shoot tips. The low Z value in plot U was definitely due to the high percentage of occupation of the shoots in the treatment subplot.

TABLE 19. The condition values of the existing shoots for which height increments were recorded and treated by subplots (Table 7-9). All recordings made during the rainy season.

Sub-plot	Date	Number shoots occupied / total	$\bar{X}$ Condition	s.d.^{2}	Z value
J-1	23 Jul.	0/29	2.603	0.471	—1.202
J-2	23 Jul.	3/38	2.342	1.185	
K-1	1 Aug.	0/266	2.537	0.338	5.416**
K-2	1 Aug.	49/149	2.875	0.411	
L-1	26 May	0/44	3.011	0.029	7.868**
L-2	26 May	28/52	3.550	0.218	
L-1	31 Jul.	0/44	2.284	0.272	7.315**
L-2	31 Jul.	38/52	3.096	0.323	
M-1	26 May	0/79	2.892	0.725	5.779**
M-2	26 May	59/88	3.522	0.246	
M-1	31 Jul.	0/79	2.329	0.755	7.120**
M-2	31 Jul.	59/88	3.212	0.523	
N-1	29 Jul.	0/81	2.456	0.207	10.205**
N-2	29 Jul.	33/56	3.650	0.248	
O-1	29 Jul.	0/38	2.421	0.331	9.601**
O-2	29 Jul.	34/34	3.602	0.223	
P-1	2 Aug.	0/61	2.327	0.182	3.130**
P-2	2 Aug.	34/46	3.000	1.988	
Q-1	30 May	0/149	3.328	0.120	0.000
Q-2	30 May	80/128	3.328	0.205	
Q-1	6 Aug.	0/149	2.318	0.142	12.477**
Q-2	6 Aug.	90/128	3.285	0.660	
R-1	28 May	14/42	2.976	0.658	—2.482
R-2	28 May	11/48	2.395	1.882	
R-1	27 Jul.	14/42	2.571	1.586	—1.895
R-2	27 Jul.	12/48	2.020	2.265	
S-1	4 Aug.	95/211	2.445	1.302	6.114**
S-2	4 Aug.	195/251	3.087	1.232	
T-1	29 Jul.	102/116	2.672	1.291	3.101**
T-2	29 Jul.	90/104	3.100	0.826	
U-1	5 Jul.	78/86	3.505	0.397	—1.701
U-2	5 Jul.	85/93	3.311	0.787	

TABLE 20. As in Table 19 (rainy season) except that recordings made during the dry season.

Sub-plot	Date	Number shoots occupied / total	$\overline{X}$ Condition	s.d.^{2}	Z value
J-1	25 Apr.	0/29	3.275	0.207	5.537**
J-2	25 Apr.	0/38	3.342	0.285	
K-1	4 Apr.	0/205	3.214	0.230	4.865**
K-2	4 Apr.	48/138	3.467	0.223	
N-1	3 Apr.	0/81	3.339	0.205	5.151**
N-2	3 Apr.	43/56	3.714	0.162	
O-1	3 Apr.	0/38	3.500	0.229	0.126
O-2	3 Apr.	32/34	3.514	0.219	
P-1	24 Mar.	8/61	3.040	0.035	—0.188
P-2	24 Mar.	28/46	3.032	0.060	
Q-1	16 Mar.	7/149	3.057	0.001	—0.041
Q-2	16 Mar.	94/128	3.058	0.088	
S-1	6 May	55/211	3.063	0.623	0.747
S-2	6 May	175/251	3.119	0.683	
T-1	8 May	50/116	3.112	0.730	1.539
T-2	8 May	78/104	3.269	0.431	

The condition records for eight plots and eight independent recordings during the cool season are given in table 20. Of the eight possible contrasts between the control and treatment subplots, three have highly significant Z values, while five other values are not significant. The high values for treatment subplots were associated in part with the production of flowering branches and in part with the lack of phytophagous insects during the dry season. In the control subplots, most of the shoots were old enough to react to the dry season by not producing vertically lengthening branches and new leaves so that their condition value was depressed.

The condition ratings for 11 plots and 13 independent recordings during the cool season are given in table 21. Of the 13 possible contrasts between the control and treatment subplots, one has a highly significant Z value and 12 do not have significant Z values. Of the 12 low Z values, 10 are minus values. This was associated with the parathion stimulation, the presence of occupied shoots in treatment subplots, the reduction in phytophagous insect activity by the cool weather, the reduction of worker activity outside of the thorns during cool weather, and the general lowering of plant growth rates by cool weather.

The condition records for two plots and two independent recordings during November 1963 are given in table 22. Both contrasts have large negative

TABLE 21. As in Table 19 (rainy season) except that recordings made during the cool season.

Sub-plot	Date	Number shoots occupied / total	$\overline{X}$ Condition	s.d.^{2}	Z value
J-1	12 Dec.	0/29	3.379	0.297	—1.408
J-2	12 Dec.	0/38	3.210	0.157	
K-1	22 Dec.	0/178	3.016	0.016	2.950**
K-2	22 Dec.	42/143	3.075	0.067	
L-1	12 Dec.	0/44	2.977	0.115	0.243
L-2	12 Dec.	7/69	2.992	0.088	
L-1	18 Jan.	0/44	3.090	0.293	—1.925
L-2	18 Jan.	20/52	2.884	0.251	
M-1	6 Dec.	27/85	3.294	0.198	—2.615
M-2	6 Dec.	54/101	3.133	0.160	
M-1	18 Dec.	6/79	3.506	0.253	—7.122
M-2	18 Dec.	59/88	2.954	0.247	
N-1	20 Dec.	35/342	3.061	0.059	—0.550
N-2	20 Dec.	44/240	3.050	0.079	
O-1	20 Dec.	9/183	3.090	0.100	—2.958
O-2	20 Dec.	31/181	3.019	0.023	
P-1	28 Dec.	0/86	3.244	0.295	0.355
P-2	28 Dec.	26/47	3.276	0.221	
R-1	9 Dec.	18/42	3.000	0.268	—7.014
R-2	9 Dec.	3/48	2.906	0.570	
S-1	11 Jan.	22/211	3.431	0.236	—7.648
S-2	11 Jan.	131/251	3.135	0.118	
T-1	6 Jan.	17/116	3.258	0.219	—4.801
T-2	6 Jan.	82/104	3.028	0.052	
U-1	21 Jan.	39/86	3.093	0.079	—3.595
U-2	21 Jan.	78/93	2.924	0.130	

Z values. The magnitude of the Z value was strongly associated with the large sample sizes. The larger values in the treatment subplots were apparently associated with parathion stimulation.

Contrasts of the condition of occupied shoots with unoccupied shoots. The condition records in tables 23 through 27 are for the same groups of continuously occupied or unoccupied shoots that were used in the comparisons of height increment for occupied and unoccupied shoots in tables 11 through 14.

1. Suckers. Table 23 presents the condition ratings for suckers that were recorded during the rainy season. All 17 of the contrasts have a highly sig-

TABLE 22. As in Table 19 (rainy season) except that recordings made before the cool season (in the end of the 1963 rainy season).

Sub-plot	Date	Number shoots occupied / total	$\bar{X}$ Condition	s.d.^{2}	Z value
M-1	14 Nov.	32/368	3.266	0.148	—260.000
M-2	14 Nov.	52/243	3.006	0.054	
O-1	14 Nov.	8/146	3.102	0.085	—27.000
O-2	14 Nov.	40/145	3.075	0.046	

nificant Z value. The contrasts for plot A on 16 Jun. and B on 23 May are presumed to be highly significant since other contrasts with similar differences have a highly significant Z value. It was impossible to apply a Z test since the s.d. is 0.0 in the control subplots.

Table 24 presents the condition records for four plots during the dry season; six of the seven possible contrasts have a highly significant Z value. The single contrasts with a significant Z value from plot C was associated with the lower condition value in the control subplot (from which most of the occupied shoots came). This value was lower because the shoots had been unoccupied since 5 Jan.; the only reason why the difference between the two means is great enough to yield a significant Z value is because there were four shoots in the plot which were occupied since 5 Jan. by auxiliary-units which had moved into the plot on their own. These four shoots all had a value of four.

Table 25 presents the condition records for three plots during the cool season; two of the three possible contrasts have a highly significant Z value and one has a significant Z value. The relatively low Z values for each contrast were associated with the small sample sizes, the relative newness of the stumps, and the high incidence of *Coxina hadenoides* in both of the plots.

Existing shoots. Table 26 presents the condition records for seven plots during the rainy season; nine of the ten contrasts have a highly significant Z value. The low Z value obtained from the contrast from plot Q was associated with the production of flowering branches on unoccupied shoots (a characteristic damage reaction), and the slow response of the occupied shoots to the beginning of the rainy season.

Table 27 presents the condition records for five plots during the cool and dry season; two of the six contrasts have a highly significant Z value. In plot L the low condition records among the occupied shoots was associated with the inactivity of the workers during the cool weather; since these were young colonies that had very recently developed in situ, they did not have many workers outside of the thorns. The same situation existed in plot M, but in

TABLE 23. The condition values of the sucker shoots for which length increments were recorded and contrasted as groups of occupied and unoccupied shoots (Tables 10-11). All recordings made during the rainy season.

Plot	Date	Number shoots	$\bar{X}$ Condition	s.d.^{2}	Z value
A un	16 Jun.	41	3.309	0.731	**
A occ	16 Jun.	25	4.000	0.000	
A un	3 Aug.	41	2.695	0.423	7.888**
A occ	3 Aug.	25	3.760	0.731	
B un	23 May	36	2.500	1.383	**
B occ	23 May	42	4.000	0.000	
B un	17 Jun.	36	2.861	0.937	4.792**
B occ	17 Jun.	42	3.714	0.245	
B un	7 Aug.	36	1.861	0.680	12.535**
B occ	7 Aug.	42	3.904	0.352	
C un	27 May	47	2.627	0.940	5.729**
C occ	27 May	16	3.687	0.229	
C un	6 Aug.	47	1.234	1.226	12.579**
C occ	6 Aug.	16	3.687	0.196	
D un	25 May	13	2.076	0.340	7.804**
D occ	25 May	22	3.590	0.253	
D un	28 Jul.	13	1.653	0.975	6.491**
D occ	28 Jul.	22	3.568	0.269	
E un	10 Jun.	39	2.692	0.878	5.338**
E occ	10 Jun.	21	3.052	0.693	
E un	7 Aug.	39	1.435	0.897	16.607**
E occ	7 Aug.	21	3.976	0.012	
F un	6 Jul.	26	2.173	0.759	6.605**
F occ	6 Jul.	26	3.461	0.238	
G un	6 Jul.	25	2.080	0.868	7.688**
G occ	6 Jul.	15	3.733	0.174	
H un	10 Jun.	79	1.734	2.130	8.747**
H occ	10 Jun.	59	3.652	0.200	
H un	5 Aug.	79	0.987	1.126	16.552**
H occ	5 Aug.	59	3.652	0.760	
I un	10 Jun.	50	1.480	1.208	16.064**
I occ	10 Jun.	36	3.986	0.007	
I un	6 Aug.	50	0.340	0.739	24.431**
I occ	6 Aug.	36	3.736	0.164	

TABLE 24. As in Table 23 (rainy season) except that recordings made during the dry season.

Plot	Date	Number shoots	$\overline{X}$ Condition	s.d.^{2}	Z value
C un	17 Mar.	47	2.552	0.828	0.794
C occ	17 Mar.	16	2.781	1.032	
E un	23 Mar.	39	2.820	0.611	3.308**
E occ	23 Mar.	21	3.442	0.417	
F un	24 Apr.	26	2.903	1.320	3.734**
F occ	24 Apr.	26	3.788	0.145	
G un	24 Apr.	25	2.980	0.760	3.139**
G occ	24 Apr.	15	3.633	0.195	
H un	11 Mar.	79	2.227	0.921	9.032**
H occ	11 Mar.	59	3.338	0.210	
I un	13 Mar.	50	1.130	1.967	12.262**
I occ	13 Mar.	36	3.791	0.276	
I un	18 Apr.	50	0.740	1.686	14.740**
I occ	18 Apr.	36	3.916	0.078	

TABLE 25. As in Table 23 (rainy season) except that recordings made during the cool season and before.

Plot	Date	Number shoots	$\overline{X}$ Condition	s.d.^{2}	Z value
F un	6 Jan.	26	2.903	0.900	2.221*
F occ	6 Jan.	26	3.365	0.231	
G un	29 Nov.	25	3.380	0.651	2.627**
G occ	29 Nov.	15	3.866	0.124	
G un	6 Jan.	25	2.880	0.443	2.475**
G occ	6 Jan.	15	3.333	0.238	

this plot there was an exceptional lack of phytophagous insects in the treatment subplot, in which most of the unoccupied shoots were located. This may have been due to one of the earlier insecticide applications. In plot P the high condition value for unoccupied shoots was associated with the production of flowering shoots. The similar condition values for the occupied and unoccupied shoots in plot S are a reflection of the production of new shoot tips by the parathion stimulation, and the lack of ants during the cool nights on the surface of shoots that are occupied during the warmer diurnal hours.

Discussion. It is evident from the data presented in tables 15-27 that the presence of the workers of a colony of *Pseudomyrmex ferruginea* on a shoot

TABLE 26. The condition values of the existing shoots for which height increments were recorded and treated by groups of occupied and unoccupied shoots (Tables 12-13). All recordings made during the rainy season.

Plot	Date	Number shoots	$\overline{X}$ Condition	s.d.^{2}	Z value
L un	26 May	49	3.061	0.058	7.758**
L occ	26 May	12	3.833	0.106	
L un	31 Jul.	49	2.295	0.290	7.185**
L occ	31 Jul.	12	3.416	0.220	
M un	26 May	77	2.915	0.779	6.766**
M occ	26 May	44	3.727	0.191	
M un	31 Jul.	77	2.324	1.157	8.598**
M occ	31 Jul.	44	3.545	0.230	
N, O un	31 Jul.	122	2.459	0.176	19.450**
N, O occ	31 Jul.	95	3.626	0.215	
P un	2 Aug.	71	2.112	0.658	12.951**
P occ	2 Aug.	34	3.705	0.198	
Q un	30 May	159	3.251	0.347	1.329
Q occ	30 May	68	3.345	0.203	
Q un	6 Aug.	159	2.267	0.223	16.077**
Q occ	6 Aug.	68	3.669	0.422	
R un	28 May	47	2.776	0.454	10.948**
R occ	28 May	17	3.441	0.246	
R un	26 Jul.	47	2.127	1.281	8.204**
R occ	26 Jul.	17	3.735	0.191	
S un	3 Aug.	143	1.744	1.118	19.586**
S occ	3 Aug.	181	3.591	0.206	

TABLE 27. As in Table 26 (rainy season) except that recordings made during the dry season or cool season.

Plot	Date	Number shoots	$\overline{X}$ Condition	s.d.^{2}	Z value
L un	18 Jan.	49	2.979	0.426	—0.210
L occ	18 Jan.	12	2.958	0.019	
M un	18 Jan.	77	3.467	1.245	—3.296
M occ	18 Jan.	44	3.045	0.015	
P un	24 Mar.	71	3.070	0.048	—1.400
P occ	24 Mar.	34	3.014	0.057	
Q un	19 Mar.	159	2.990	0.102	2.476**
Q occ	19 Mar.	68	3.095	0.084	
S un	11 Jan.	143	3.325	0.207	—3.115
S occ	11 Jan.	181	3.182	0.138	
S un	5 May	143	2.772	1.240	5.707**
S occ	5 May	181	3.337	0.208	

TABLE 28. The distribution of significant Z values among contrasts of condition values of *Acacia cornigera* made at different times of the year. Note that the highest frequencies of Z values are associated with recordings made during the rainy season of subplots, or groups, of suckers from stumps.

Table	Time of year	Number of contrasts	Number highly significant contrasts	Number significant contrasts	Number not significant contrasts	Type of shoots
(treated as subplots)						
15	rainy	28	17	4	7	suckers
16	dry	13	7	1	5	suckers
17	cool	7	4	0	3	suckers
18	rainy 1963	5	1	1	3	suckers
19	rainy	16	11	0	5	existing
20	dry	8	3	0	5	existing
21	cool	13	1	0	12	existing
22	rainy 1963	2	0	0	2	existing
23	rainy	17	17	0	0	suckers
24	dry	7	6	1	0	suckers
25	cool	3	2	1	0	suckers
26	rainy	10	9	0	1	existing
27	cool & dry	6	2	0	4	existing

of *Acacia cornigera* has an effect on the condition of the shoot. In view of the dependent relation between height increment and the condition of the shoot, this result is expected. It seems clear that the same variables in the environment that affected the height increments of occupied and unoccupied shoots also affected the condition of these shoots. This is clear from table 28. The two tables are quite similar in respect to the temporal and bionomic location of the significant Z values; the highest numbers of significant Z values are yielded by contrasts of recordings made during the rainy season and among suckers from stumps cut during the experimental program. In addition, tables 14 and 28 show that the treatment of shoots as unoccupied and occupied groups in contrast to subplot comparisons, show more clearly the effect of the ants on the shoot.

The lowered frequency of significant Z values in subplot contrasts is due to the same factors as is the case with subplot contrasts of height increment. It appears that the contrast of condition values from groups of consistently occupied and unoccupied shoots is just as sensitive as the contrast for height increment values in showing the influence of *P. ferruginea*. In fact, if the condition records are made at the beginning of a period of growth, they may show significant differences in the condition between groups of occupied and unoccupied shoots before significant height increments can accrue.

TABLE 29. Mortality of occupied and unoccupied stumps and their suckers of *Acacia cornigera* in plots H, I and E during 1963-1964. These data are grouped by subplots and this is associated with the high mortality shown in control subplot I-1 before the 1964 rainy season began; those stumps which died in I-1 were almost all unoccupied.

		Treatment (1)		Treatment (2)		Control (3)	
Sub-plot	Date	number alive	number dead	number alive	number dead	number alive	number dead
H-1, H-2, H-3	17 Oct.	43	0	66	0	72	0
	11 Mar.	35	8	61	5	71	1
	10 Jun.	27	16	53	13	71	1
	5 Aug.	23	20	48	18	71	1
I-1, I-2, I-3	18 Oct.	38	0	31	0	39	0
	13 Mar.	22	16	21	10	34	5
	10 Jun.	18	20	17	14	28	11
	6 Aug.	17	21	13	18	28	11
E-1, E-2, E-3	18 Nov.	29	0	24	0	21	0
	23 Mar.	27	2	23	1	21	0
	10 Jun.	27	2	19	5	21	0
	7 Aug.	24	5	14	10	21	0

Ratings of condition of heavily occupied shoots during the rainy season furnish a very good indicator of the density of the two insects which are relatively insensitive to *P. ferruginea,* and eat shoot tips: *Coxina hadenoides* and *Pelidnota punctulata.* It appears that if these two insects are not present during the rainy season, nearly every occupied shoot will maintain an undamaged terminal shoot tip (a 4 condition rating), and show a resultant high height increment. The condition ratings of completely unoccupied shoots appear to be a good indicator of the density of insects that feed on *A. cornigera* at all times in the year; the rating values increase during the dry season, and then drop very rapidly when the rainy season starts.

Mortality of A. cornigera. Greater mortality occurred among sucker shoots from stumps cut during the study, than among existing shoots. While this was in part due to a greater susceptibility of sucker shoots, and the stump from which they came, to cumulative insect damage, it was also associated with the problem that none of the treatment subplots of existing shoots were free from occupation until the 1964 dry season. On the other hand, plot H, I, and E had treatment subplots that were relatively free of ants from their time of cutting in Oct.-Nov. 1963 to the end of the experiment in August 1964. The mortality of shoots in these plots is presented in table 29.

It should be emphasized that when a shoot is recorded as dead in table 29, it means that the stump as well as the sucker is dead. In most cases, the root system appeared to be dead as well. The death of the shoots in these three plots appeared to be associated entirely with the cumulative effect of continuous insect damage to the inner bark and foliage. In all three plots, every stump produced at least one new branch and usually many more before it died. The larvae of *Chrysobothris* sp., near *C. multistigmosa* were found in nearly every dead stump during the August recordings.

It was often the case that a newly cut stump produced a cluster of 5-15 new branches within six weeks after being cut. If the shoot is occupied, one of these usually becomes the main axis of the shoot and grows rapidly upward. If the shoot is unoccupied, the shoot tips of these branches are usually eaten within a few days to a week after their appearance. The stump continues to produce new shoots but at a rapidly decreasing rate and within several months becomes nearly dormant. From this stage, it is killed after a variable number of months by the internal girdling activity of *Chrysobothris* sp., near *C. multistigmosa.* However, in plot B there was a cluster of five unoccupied stumps in the relatively dormant stage following defoliation, which became occupied by a large colony from a large cut shoot in May. By August, these stumps had main sucker shoots 50-85 cm in length. It appears that occupied stumps with vigorous suckers are not always killed by the larvae of *Chrysobothris* sp., near *C. multistigmosa,* since these five stumps had been infested.

The data presented in table 29 for three plots can be considered as representative of the fate of occupied and unoccupied stumps. However, shoots from which the ant colonies are removed by clipping the thorns or spraying, still have their crop of mature leaves and therefore are more slow to die; these leaves are only slowly removed by phytophagous insects. In addition, the ability of an unoccupied shoot to continue to produce new shoot tips, even when they are being rapidly destroyed, appears to be stronger among existing shoots than among suckers from stumps. For example, between 3 Apr. and 29 Jul., the 81 unoccupied shoots in treatment subplot N-1 produced 328 new vertically lengthening branches which could have become central axes. Every one of them had its shoot tip eaten off before it was more than 25 cm long. It is very unlikely that any equal sized group of cut stumps that had been unoccupied for the length of time that those in N-1 were (116 days), would have produced anywhere near this number of new shoots. It should be noted that while occupied suckers from stumps tend to grow almost continuously for the first six months to a year after the stumps are cut, existing shoots often respond to the cool and dry season by not producing new growth. Therefore, new growth is not present to be destroyed by phytophagous insects if the shoot is abandoned by an auxiliary-unit.

One aspect of the mortality of existing shoots is due to the feeding behavior of the rodent *Sigmodon hispidus.* In no case was an occupied shoot found that had been cut and fed on by *S. hispidus;* during the later part of the dry season, it was a relatively common case to find a deep notch cut by this rodent in the trunk of an occupied shoot a few cm above the ground. While workers of *P. ferruginea* were never observed to turn one of these rodents away, it appears that this is what occurred. *S. hispidus* only cuts shoots of a basal diameter of about 1.5 cm or less. Thus, it confined its activity to the small unoccupied shoots; these shoots were usually below the canopy of the general vegetation. Once a shoot became occupied and began vigorous growth, its basal diameter became so great that *S. hispidus* generally did not try to cut it even if it was unoccupied. Occasionally, *S. hispidus* climbed into the canopy of 1.5-2 m tall unoccupied shoots and cut off the short new branches which were then eaten on the ground. The damage of the rodent to unoccupied shoots became increasingly severe as the dry season progressed but stopped almost entirely after the first rains caused new growth among other plants.

In plots such as P and S, *S. hispidus* was responsible for the removal of better than 50 per cent of the short unoccupied shoots during the dry season. New shoots often grew from these stumps when the rains started or shortly before, but they were so heavily shaded that they had almost no height increment. These shoots were also heavily damaged by the insects which commonly fed on unoccupied *A. cornigera*. It should be re-emphasized that although *S. hispidus* was the only common rodent in the area of the rodent damage, an individual was never collected while feeding on *A. cornigera*, though three were seen while feeding on it. The damage described above may have been caused by some other species of rodent which is very similar to *S. hispidus* in appearance. However, specimens of *S. hispidus* fed rapidly on *A. cornigera* in the laboratory.

There was no evidence of direct biotic mortality factors of *A. cornigera* in natural disturbance sites that were absent in man-made disturbance sites. The opposite situation was also the case. However, the density of an animal such as *S. hispidus* was definitely higher in man-made disturbance sites than in any natural disturbance sites in the area between Temascal and La Granja.

Leaf production by A. cornigera. The number of leaves on a shoot of *A. cornigera* is a function of how many are produced and how many are removed. Unoccupied suckers from stumps and existing shoots produce fewer leaves and have more removed by phytophagous animals than do occupied shoots. They produce fewer leaves because the continual defoliation of the shoot weakens it. The phytophagous animals in the experimental plots were insects and occasionally the rodent *Sigmodon hispidus*. In those plots, and at those times when cattle were present, their direct defoliating activity was almost nonexistent. This latter statement applies to both unoccupied and occupied shoots. A leaf had to be at least one-half intact to be counted in the following four examples recorded in July and August 1964.

(1) On 29 Jul. the 81 unoccupied shoots in treatment subplot N-1 had a mean number of 88.59 leaves per shoot (s.d.=45.4 leaves). On the same date, the 69 occupied shoots in control subplot N-2 and O-2 had a mean number of

183.23 leaves per shoot (s.d.=245.3 leaves). However, control subplot N-2 contained one exceptional shoot with 2,000 leaves on it. If this shoot is excluded, then the mean number per occupied shoot becomes 156.51 leaves (s.d.=105.3 leaves). A Z test of the mean of 68.59 contrasted with 156.51 yields a highly significant Z value (8.108). The high s.d. of the number of leaves on the occupied shoots was in great part associated with the presence of six shoots which had just recently had their leaf crop eaten off by the larvae of *Syssphinx mexicana.* Virtually all of the leaves counted in the above subplots were produced by the shoots after 31 Dec. Most of them were produced after 1 May. In the treatment subplots, nearly all of them were from the axils of swollen thorns produced when the shoots were occupied in 1963. In the control subplots, most of the leaves were borne on new swollen thorns on lateral branches produced in 1964.

(2) The stumps in plot A were cut on 25 May 1964. By Aug. 1964 the 42 unoccupied shoots in treatment subplot A-1 had produced 1,458 leaves and 1,016 swollen thorns. The 29 occupied shoots in control subplot A-2 had produced 4,818 leaves and 3,774 swollen thorns. Less than 10 per cent of the leaves and swollen thorns on the unoccupied shoots were produced after 1 July; at least 50 per cent of the leaves and swollen thorns on the occupied shoots were produced after 1 July.

(3) The stumps in plot H were cut on 17 Oct. 1963. By 5 Aug. 1964, the 66 shoots in treatment subplot H-2 had produced 3,460 leaves and 2,596 swollen thorns. The 72 shoots in control subplot H-3 had produced 7,785 leaves and 7,483 swollen thorns. The high number of leaves produced in the treatment subplot H-2 was in part associated with the presence of 30 new colonies which had developed in situ, and which occupied the shoots during the month of July. It was also associated with some growth that occurred during the last month of the dry season when there were almost no active phytophagous insects in the plant community.

(4) The stumps in plot D were cut on 10 Dec. 1963. Due to the proximity of uncut shoots with large colonies of *P. ferruginea,* a number of the shoots in the treatment subplots became occupied. Because of this, the shoots were segregated in the recording and the leaves were counted as 1) those on occupied shoots and 2) those on unoccupied shoots when the final recording was made on 28 Jul. 1964. The 14 unoccupied shoots had produced a total of 321 leaves and 128 swollen thorns. The 26 occupied shoots had produced a total of 2,391 leaves and 1,578 thorns. In comparing the leaf and swollen thorn production in this plot with that in plot B the effect of the dry season, even on stumps, can be seen. The plants in plot D were nearly six months older than those in plot A but plot D still had a lower mean number of leaves and swollen thorns per shoot. Most of the six month lead was during the dry season. This effect is also in part due to the fact that the shoots in plot D were partially shaded while those in plot A were receiving full sunlight.

On the basis of the above 4 examples, it is clear that a colony of *P. ferruginea* has a definite effect on the number of leaves borne by a shoot of *A. cornigera.* In addition, the colony has a much better opportunity for growth on an occupied shoot, than on an unoccupied shoot. On an occupied shoot, it has both more living space and more food available to it since each new leaf means a new crop of Beltian bodies, another source of nectar, and often a new swollen thorn.

Biomass production of A. cornigera. In the plots with sucker regeneration from cut stumps, it was possible to harvest the crop of shoots and weigh them. An insignificant error was introduced by the weight of the ants living in the thorns. The shoots were weighed within 24 hours after being cut; the shoots from the various groups within a plot were all weighed after the same time interval. The original stumps were not weighed. The following five examples of biomass production by occupied and unoccupied shoots are representative of that which occurred throughout the experimental plots.

(1) The stumps in plot A were cut on 25 May. By 13 Aug., the 42 shoots in treatment subplot A-1 weighed 850 gm; the 29 shoots in the control subplot A-2 weighed 7,750 gm. (2) The stumps in plot B were cut on 29 Apr. By 7 Aug., the 36 unoccupied shoots weighed 450 gm; the 64 occupied shoots weighed 43,650 gm. (3) The stumps in plot D were cut on 10 Dec. 1963. By 28 Jul. the 14 unoccupied shoots weighed 365 gm; the 26 occupied shoots weighed 4,810 gm. (4) The stumps in plot E were cut on 26 Nov. 1963. By 7 Aug. the 29 shoots in treatment subplot E-1 weighed 3,690 gm., the 24 shoots in treatment subplot E-2 weighed 11,240 gm., and the 21 shoots in control subplot E-3 weighed 31,212 gm. (5) The stumps in plot H were cut on 17 Oct. 1963. By 5 Aug. the 66 shoots in treatment subplot H-2 weighed 2,900 gm; the 72 shoots in control subplot H-3 weighed 41,750 gm (weights for treatment subplot H-1 were not recorded because the thorns had been clipped).

Comparisons of the weight of occupied shoots with unoccupied shoots show stronger differences than comparisons of the number of leaves or swollen thorns. This is due for the most part to several factors. The leaves on occupied shoots are usually large and completely intact in contrast to the leaves on unoccupied shoots which are usually smaller and damaged to some degree. The thorns produced by occupied shoots are fully developed while the thorns on unoccupied shoots are often partly eaten while still green. The leaves on occupied shoots are for the most part produced during branch elongation and bear very large swollen thorns; the leaves on unoccupied shoots are often from the axils of older thorns and have minute stipules. The number of meters of branch length is much greater on occupied shoots in contrast to unoccupied shoots. Those branches that are present on unoccupied shoots are very thin in contrast to the thick branches on most of the occupied shoots.

Observations of the plots with cut stumps in them showed that a single heavily occupied stump of *A. cornigera* produces far more woody vegetation and height increment in the first year of regeneration than does a single stump of any other species of plant in the plots. This was true in respect to both maximum and mean values. However, some plants such as *Bixa orellana* and *Croton glabellus* produced a higher amount of woody vegetation per hectare because of their very high density of shoots. On the other hand, it also appears that a single unoccupied stump of *A. cornigera* produces less vegetation in the first and following year than does a single stump of any other tree species in the plots. This was true in respect to both maximum and mean values. This marked superiority of growth rate enjoyed by occupied *A. cornigera* slowly diminishes after the end of the first year of regeneration, although the effects of this early burst of growth are indicated by the emergent position of the shoot for nearly its entire life.

Presence of vines. While annual and perennial vines constituted a major part of the regeneration in many of the experimental plots, it was extremely rare to find one using a shoot of *A. cornigera* for a standard (Fig. 60, 61). If a vine was well established on *A. cornigera,* the shoot was an unoccupied one or the ants had recently invaded the shoot as an auxiliary-unit, or as a colony developed in situ. The tips of the vines are usually killed by the ants as soon as they contact occupied shoots (Fig. 34, 37b); when growing up through a vine mat, the shoot is often ringed by blackened vine ends.

In the experimental plots, it was common to find undamaged vines growing in the canopies of unoccupied shoots of *A. cornigera.* The number of vines and the degree to which they pulled the shoot over, or shaded it, was in great part associated with the type of plant community. Unoccupied shoots in areas browsed by cattle were often free of vines because the cattle removed them from the shoots. When the canopy of *A. cornigera* was part of a dense general canopy, vines often grew completely over it when the ants were removed. Since this acacia is so intolerant of shading, this is an obvious handicap. The following four examples give a representative indication of the incidence of vines on occupied and unoccupied shoots.

(1) On 31 Jul. 1964, the 88 shoots in control subplot M-2 (59 occupied shoots) had 34 vines on 10 of the shoots; none of these 10 shoots were occupied. In treatment subplot M-1, the 79 unoccupied shoots had a total of 158 vines on 52 of the shoots. In both subplots, most of these vines were in the families Passifloraceae, Convolvulaceae, and Leguminosae. These vines had been accumulating on the unoccupied shoots since late in 1963. In some cases (Convolvulaceae, Leguminosae), they had flowered and set seed during this period. Many of the unoccupied shoots were completely covered with vines and the thinner shoots were often bent by the weight of the vines.

(2) On 24 Mar. 1964, the 46 shoots in control subplot P-2 (28 occupied) had no vines on them. On the same date, the 61 shoots in treatment subplot

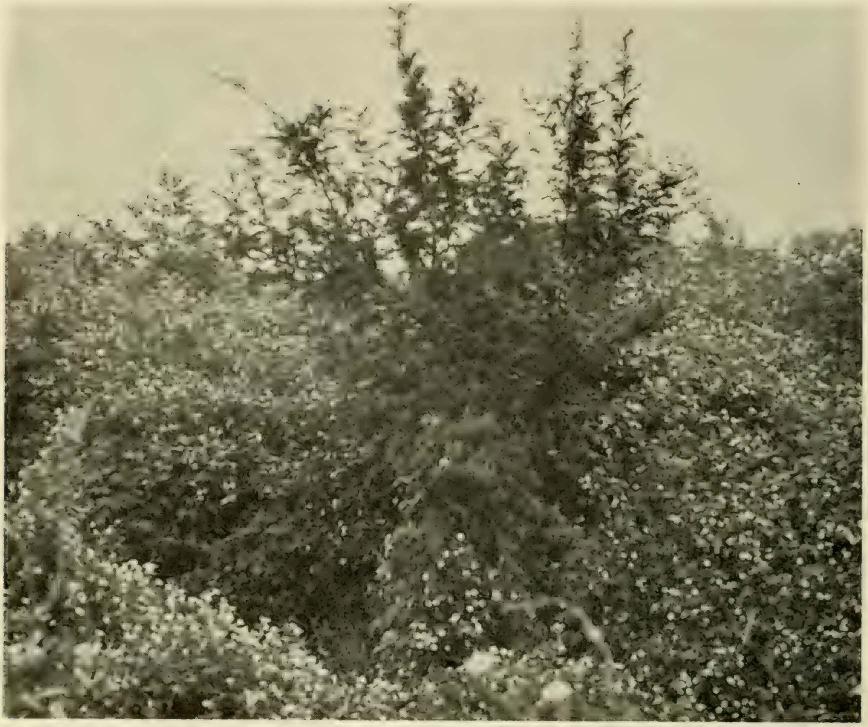


FIG. 60. The usual freedom from vines exhibited by occupied shoots of *A. cornigera.* The 3.5 m tall shoot in the center of the photograph is about 3 years old and growing in a roadside mat of *Ipomoea* sp. The white flowers of this vine are scattered over the canopy. This shoot of *A. cornigera* was ringed by at least 50 dead vine leaders that had been killed by *P. ferruginea.* Photo 10 km north of Tierra Blanca, Veracruz, Mexico in November 1963.

P-1 (7 occupied) had one vine on them. By 2 Aug., the 46 shoots in control subplot P-2 (34 occupied) still had no vines on them. On this date, the 61 shoots in treatment subplot P-1 (0 occupied) had a total of 129 vines on 35 shoots. Most of these vines were in the Asclepiadaceae, Sapindaceae, Menispermaceae, Bignoniaceae, Convolvulaceae, and Leguminosae. They were all present in large numbers in the control subplot but their branches had been killed when they started to enter the canopies of the occupied shoots of *A. cornigera.* In the treatment subplot, the vines had formed a solid mat over the tops of many of the occupied shoots; the result was that under casual observation the density of *A. cornigera* in the treatment subplot appeared to be very low. The lack of vines on unoccupied *A. cornigera* during the dry season was due to the general lack of growth of most vegetation in the plot, plus the fact that the shoots in the treatment subplot were occupied until the thorns were clipped.

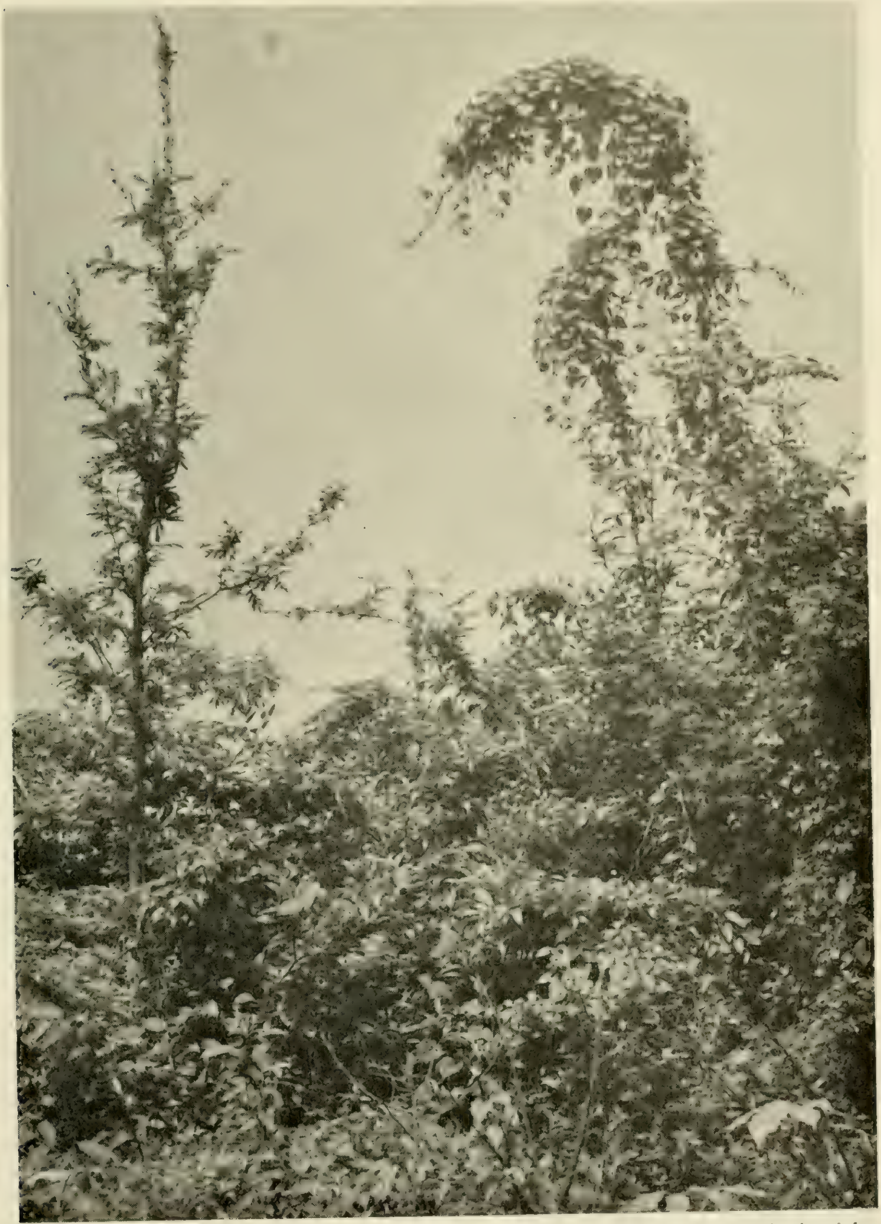


FIG. 61. The left-hand shoot is occupied by a large colony of *P. ferruginea* while the right-hand shoot is unoccupied. The unoccupied shoot is festooned with a number of vines of the Convolvulaceae; the upper part of the shoot has been bent over by the weight of the vines. In addition, the foliage of this shoot was very badly damaged by insect attack. The vines have attempted to enter the occupied shoot a number of times as can be seen by the large number of vertical and dead, bare tendrils among the lower branches. Photo 2 Aug. 1964 along roadside east of Temascal.

(3) On 3 Apr. 1964, both the occupied and unoccupied shoots in plots N and O were completely free of vines; this was due to the low amount of growth in the plots during the preceding eight months plus the fact that the shoots were for the most part occupied during the previous rainy season. By 29 Jul. 1964, the 119 unoccupied shoots in the two treatment subplots had a total of 153 vines on 54 shoots. There were no vines on the 90 shoots in the two control subplots (N-2 and O-1). The taller unoccupied shoots were lightly draped with vines, but some of the shorter shoots were completely tied into the general vegetation by the vines. These vines were in the Convolvulaceae, Asclepiadaceae, and Leguminosae.

(4) On 4 Aug. 1964, there were 290 occupied shoots among the 462 shoots of *A. cornigera* in plot S. None of the occupied shoots had vines in their canopies. There was a total of 150 vines on 61 of the unoccupied shoots. The relatively low number of vines was associated with the slow vegetation growth during the dry season, and the relatively low number of vines in the vegetation in plot S in comparison with other similar plots.

The vines in the experimental plots covered unoccupied *A. cornigera* to a much greater extent than other species of woody plants; the vines tended to form larger clusters on the emergent unoccupied *A. cornigera* and bind them into the general canopy (Fig. 61). This was due to the prevention of further growth of the unoccupied shoots and their relatively stiff woody form with thorny branches that served as an excellent support for the vines. Furthermore, the emergent shoots of *A. cornigera* that became unoccupied for some reason, were usually the tallest plants in regeneration less than four years old, and therefore were the most suitable for climbers by virtue of their position in the vegetation.

Presence of basal circles. While normally occupied shoots are nearly always free of foliate intrusive vines or branches of other plants, the circular area around the base of occupied shoots (Fig. 35) is much more variable in respect to the degree of damage to the vegetation by *P. ferruginea.* This variation in the size and cleanliness of the basal circle is associated with the size of the colony, type of vegetation under the *A. cornigera,* length of time that the colony has occupied the shoot, and the height of the shoot canopy above the ground. In addition to these four factors, there is variation that appears to be due to the individual behavior of the colony itself.

Large colonies often have well defined, large, and clean basal circles under their shoots. A basal circle is usually not evident until the portion of the colony in the shoot has 500 or more workers. The larger the colony, the more workers patrol and/or clean on the soil under the shoot. The longer it has been in the shoot, the more likely it is that the ants have had time to produce a very clean and well defined basal circle.

The type of vegetation under the shoot to some extent dictates how long is required for the ants to kill the vegetation, or stop it from producing new leaves. Seedlings are killed almost immediately after appearing above the soil, while on existing woody stems, the new leaves have to be repeatedly destroyed. As the shoot grows, the canopy is carried upward, and the colony is located further and further above the ground. As this occurs, the density of workers in the basal circle decreases. When a canopy is over 5-7 m above the ground, there is usually little trace of the basal circle. However, vines attempting to enter the canopy are attacked with the usual aggressiveness.

The cleanest and largest basal circles are found under shoots that are in their second to fourth year of occupied growth, and are growing over grass, herbs or low leafy shrubs. In a site such as that which contained plots C, H, I, U and V, the basal circles varied from 30-150 cm in diameter around single shoots and up to 4 m in diameter where the basal circles of several shoots overlapped. These basal circles were characteristically bare dirt with a light to heavy even litter of pinnules, thorns and twigs from *A. cornigera.*

There are a number of facts that indicate that the basal circle is the result of the workers' mauling activity of growing vegetation, and not the result of a toxicant released by *A. cornigera.* 1) In the treatment subplots, after the first two months of rainy season growth had taken place, there was total obliteration of the basal circles under the shoots that had been rid of their ants by parathion or other experimental means. This rapid loss of basal circles was due to the sprouting of both monocotyledonous and dicotyledonous seedlings, and the leafing out of the branches of low perennial shrubs and vines. 2) Not all occupied shoots have basal circles. Even when the colony is large, has been in the shoot for a year or more, is close to the ground, and is over a grass ground layer, the basal circle is not always present. 3) When a large shoot is cut and the canopy left across the stump, the colony disorganisation in the following 3-6 months is sufficiently great that the old basal circle usually becomes obliterated by seedlings and vine sprouts. 4) Finally, the workers are very often observed mauling young leaves or seedlings in the basal circle.

Seeds were planted in basal circles on two occasions to examine experimentally the activity of the ants. On 3 Aug. 1962, near Campo Cotaxtla, Veracruz, a 250 cm isolated queen-shoot with a large colony was chosen in a lightly grazed grass pasture. It had a roughly circular basal circle about 110 cm in diameter. Three rows of seeds (one each of corn, beans, and radishes) were planted, radiating from the trunk to the margin of the basal circle, and extending 20 cm into the surrounding grasses. On 13 Aug. 1962 there were no seedlings left alive within 6 cm of the trunk. From this point outward the beans increased gradually in height to the margin of the basal circle; from the margin to the end of the row they were 8-10 cm tall. On this date, the row of corn was in discontinuous segments with seedlings 1-3 cm tall out to the margin of the circle; the last 20 cm of the row had plants 10-14 cm tall. Only about ⅓ of the radish row had live plants, and they were 1-2 cm tall; outside the basal circle they were 3-5 cm tall. The mauling damage to the growing points of all three species of plant was clearly evident, and the workers were seen chewing on the shoots. On 27 Aug. 1962, the beans were completely absent to a distance of 25 cm from the trunk, the corn row to 35 cm, and the radish row to 50 cm. Those plants growing outside the basal circle were all over 10 cm tall and in excellent condition.

During the 1964 rainy season, in the vegetation along the west margin of plot C, this type of experiment was repeated. The seeds of *Bixa orellana*, *Bauhinia ungulata*, *Acacia chiapensis*, *Acacia cornigera*, *Mucuna pruriens*, *Cassia bicapsularis* and *Ipomoea* sp. were planted in seven radiating rows from the base of each of eight large queen-shoots with basal circles ranging from 75-150 cm in diameter. The seeds of *B. ungulata*, *A. chiapensis* and *A. cornigera* were scarified by cutting off a piece of the seed coat. All of the seeds germinated in large numbers except *B. orellana*. The trunks of four of the shoots were banded with a 10 cm band of tree banding compound which stopped ant traffic to and from the ground. In the basal circles of the unbanded shoots, the sprouting seedlings were killed within eight days of the time that they appeared. Most were killed almost as soon as they appeared above the ground. The sprouts of *Mucuna pruriens* and *Cassia bicapsularis* were very tough and lived longer though they stopped growing upward as soon as the shoot apex was destroyed; it is the shoot apex which is usually attacked first by the workers. Outside of the basal circles, the seedlings survived and grew well. In the basal circles of the banded shoots, about three-fourths of the seedlings were damaged or killed by the mauling of workers that had fallen from the shoot, and that came to the base of the queen-shoot from nearby auxiliary-shoots. However, it took a month (July) for the basal circle to be completely cleaned of the seedlings; in one basal circle, a grass stem fell against the trunk above the band and the workers used this as a path to the ground. An unexpected result of this experiment was the discovery that the seedlings of *A. cornigera* and *A. chiapensis* were destroyed. Yet, small shoots of *A. cornigera* and *A. chiapensis* that have attained the usual characteristics of older swollen-thorn acacias, are treated like the parent shoot.

The significance of the basal circle to either the ant or the shoot is difficult to state clearly. The removal of vines and branches of other plants from the canopy of *A. cornigera* by the ants serves to avoid shading of the shoot, avoid mechanical bending of it or its branches, and remove possible highways of approach for phytophagous insects. None of these factors apply as clearly in the case of the basal circle. However, to a lesser degree the production of the basal circle furthers these purposes. The production of the basal circle by the workers can also be regarded as merely a downward extension of the workers' activity in mauling intrusive foliage in the canopy of *A. cornigera*. However, a big difference between the two activities is that when mauling a vine, the worker either maintains direct contact with the shoot or at best, is only a few centimeters from it. It does not range more than 15 to 20 cm past the shoot canopy in this activity. However, when the worker is mauling vegetation on the ground, it may walk out as far as 75 cm from the nearest part of the shoot. The possibility that the worker is obtaining something of nutritive value from the plant cannot be examined with the data at hand; but if this is to be the case, why does the worker stop its mauling activity when only a relatively short distance from the host shoot?

During the dry season, there is some evidence that the presence of a well developed basal circle can affect survival of the shoot and/or colony during fires (Fig. 22, 23). When the shoot is part of a dense stand of dry vegetation, a fire is generally strong enough to completely destroy, or at least to kill, both the colony and the shoot. However, when the surrounding vegetation is 2 m or less tall, there is a well developed basal circle, and the shoot of *A. cornigera* is sufficiently emergent so that most of the canopy is above the surrounding canopy, the heat is often not intense enough to kill the ant colony. It usually kills the shoot of *A. cornigera* by scorching the lower trunk, rather than by actually burning the canopy. In some cases, the fire does not even get hot enough to kill the shoot. In most of these cases of shoot or colony survival, there is a very large and clean basal circle in which there has been no fire. It is likely that the complete lack of inflammable materials directly under the shoot lowers the temperature in the canopy sufficiently so that the ant colony is not killed.

The survival of the ant colony, or portion of the colony, in the scorched shoot is of very great importance to the total plant; the entire ant colony is available to move into the new sucker shoots that appear within a week after the fire. An example of this is as follows. On 19 May 1964, about 15 acres of 15 month old ungrazed regeneration were burned along the east side of the plots C, H, and I. On 11 Jul., an area 100 by 40 m was marked out in the center of this burn. There were 365 standing tall shoots in this area; the small shoots had been completely consumed by the fire. Of these 365 shoots, 96 were dead and had no new suckers from the base. There were 26 shoots that had not been killed; all of these had canopies in full leaf and were occupied. Nearly all of them had well developed basal circles. The remaining 243 shoots had been killed by scorching but new suckers were growing from the old root stocks. Of these, 123 were occupied by portions of mature colonies that had survived the fire. The sucker shoots from the root stocks of these 123 shoots had a mean height of 59.66 cm (s.d.=24.9 cm). The single tallest sucker from each root stalk was measured. The mean condition rating of these 123 shoots was 3.731 (s.d.=0.383) (Fig. 22). The remainder of the 243 shoots (120 shoots) were not occupied, but some of the swollen thorns had founding queens in them. These unoccupied shoots had a mean height of 18.08 cm (s.d.=11.2 cm). The mean condition of these 120 shoots was 2.533 (s.d.=0.750) (Fig. 23).

All of the damage to the unoccupied shoots was from phytophagous insects. While the first vegetation in this area following the fire was a dense stand of grasses, the various perennial species' roots were beginning to produce a dense stand of suckers by the middle of July. Almost every unoccupied shoot was in the dense shade of this 50-75 cm tall vegetation while at least the shoot tip of nearly all the occupied shoots was a member of the canopy or was emergent. The vigorous growth of the occupied shoots, in contrast to that of the unoccupied shoots, can be attributed to the fact that there were usually 100-500 workers on the surface of a shoot that had at most three shoot tips and 20 mature leaves. That there were large numbers of workers available to patrol the shoots is in great part due to the emergent position of the occupied canopies and large basal circle before the fire. See Janzen (1967b) for further discussion of this topic.

ADDITIONAL OBSERVATIONS. *Development of colonies in situ.* When a plant community was burned by a sufficiently hot fire to kill all the colonies of *P. ferruginea* in the canopies of *A. cornigera,* the new ant colonies on the site must either develop in the new regeneration, or invade from the margins of the burn. When the colonies invade, the resultant effect on the biology of *A. cornigera* is little different from the case where the vegetation is only cut and the colonies not destroyed. However, if the colonies develop in the shoots (in situ) the pattern of regeneration of *A. cornigera* is quite different.

One of the abandoned experimental plots simulated the case of a burned site in which most of the colonies developed in situ. In plot KA the vegetation was cut to ground level on 1 Oct. 1963. In treatment suplot KA-1, the new shoots of *A. cornigera* were sprayed with parathion on 26 Oct. and 21 Dec., but due to the high density of founding queens and the invasion of two colonies from outside of the subplot, the applications had little effect on the interaction of the ants with *A. cornigera.* In each of the two control subplots (KA-2, KA-3) there were large numbers (200 plus) of new shoots from old small stumps exposed by the cutting, but only 22 were occupied by the four large colonies that had survived the cutting. These four colonies stayed in these 22 shoots and did not move out to occupy more shoots during the experiments.

During the period from 1 Oct.-1 Aug. 1964, the vegetation in the three subplots rose gradually until there was a very dense undulating canopy of grasses, herbs and shrubs 75-120 cm in height. Part of the slowness of growth of the general vegetation was associated with the very heavy grazing and trampling by cattle until 3 May 1964. On this date, the general vegetation had a mean height of about 20 cm. Likewise, on this date the mean height of the unoccupied shoots of *A. cornigera* was about 20 cm. The mean height of the shoots that had been occupied by the mature colonies since late 1963 had a mean height of about 55 cm. There were some shrubs such as *Tournefortia* *hirsutissima, Bixa orellana* and *Croton glabellus* that grew to 50-100 cm before the cattle left; like *A. cornigera,* the cattle almost never browsed these three species of shrubs.

By 1 Aug., the population of *A. cornigera* in the three subplots was very easily segregated into two groups, occupied and unoccupied. There were 99 occupied shoots. Of these 99 shoots, 28 were occupied by the six ant colonies which had been in the 3 subplots since late 1963. These colonies had moved into the shoots as large, well developed colonies and began patrolling the shoots immediately. The remaining 71 shoots were occupied by 53 small queen-units that had developed in situ. Each colony had 50-250 workers in it. There were 18 of the shoots occupied as auxiliary-shoots. At this time, there were 253 unoccupied shoots in the plot KA. The occupied shoots ranged from 63-189 cm in height with a mean height of 95.9 cm (s.d.=23.6 cm); they were all canopy members or emergents (Fig. 62). The unoccupied shoots ranged from 6-100 cm in height with a mean height of 42.58 cm (s.d.=18.9 cm); nearly all of them were below the canopy and many were in the dense shade under the canopy. The occupied shoots had a mean condition rating of 3.611 (s.d.=0.515) and the unoccupied shoots had a mean condition rating of 2.185 (s.d.=0.877). The 99 occupied shoots weighed 10,790 gm and the 253 unoccupied shoots weighed 5,410 gm.

The young queen-units which had developed in situ began to have workers patrolling the shoot tips about the middle of May. During the dry season, their biggest contribution was to remove the larvae of the gelichiid web spinner *Aristotelia corallina* from the shoot tips. When the rains started, the surrounding vegetation began to grow upward and the density of phytophagous insects increased rapidly. The workers at this time were effective in keeping these insects away except for the larvae of *Coxina hadenoides.* Since the shoot tips remained intact, the occupied shoots were able to keep up with the rising general canopy, and in some cases, to rise above it. The young colonies were very small and there were only 25-75 workers on the shoot. However, the shoots were also very small and therefore a few workers could patrol them quite effectively.

Based on observations made of other similar regenerating vegetation, probably less than 10 percent of the shaded unoccupied shoots would ever have become canopy member or emergent shoots. If the vegetation were to be cut again, these shoots, or the shoots from their roots, would have had another chance to become occupied and experience vigorous growth. It could be seen from plot KA that if an area were cleared every 1-4 years (burned and/or cut), the occupation by *P. ferruginea,* and the consequent opportunity to grow a vigorous shoot, would be rotated among the various root stocks of *A. cornigera.* It appears that often the same root stocks bear the occupied shoots after each cutting, since the cut canopy is usually left across the cut stump, and the root stocks that have recently borne an occupied shoot are probably the health-

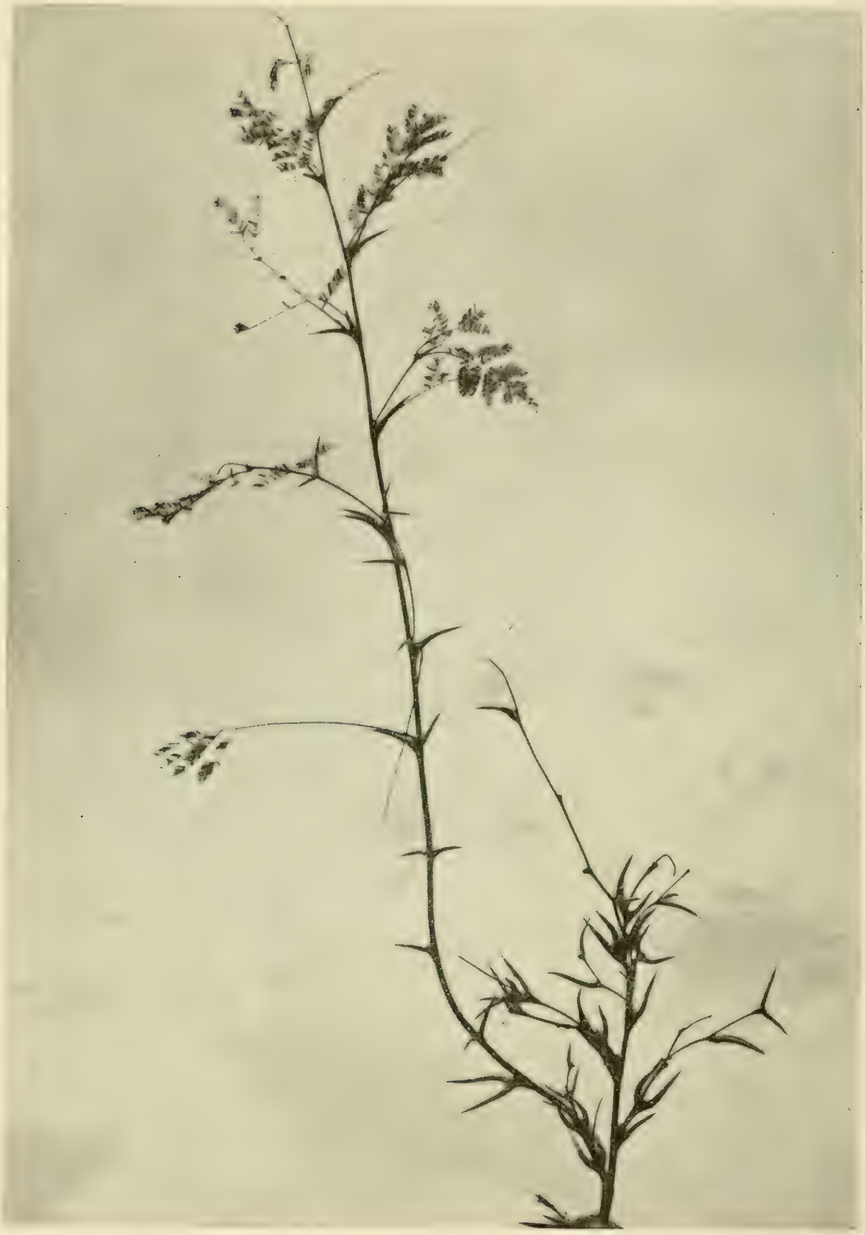


FIG. 62. A shoot of *Acacia cornigera* from control subplot KA-3. It is occupied by a small colony that developed in situ during the preceding nine months. The cluster of leafless branches in the lower part of the photograph was below the canopy and grew before the colony began to patrol the shoot. The long branch extending up to the left is the branch that grew after the workers began to patrol the shoot surface. The loss of mature leaves and shoot tip was due to nocturnally active phytophagous insects; young colonies tend to decrease their meager patrolling after dark. Photo 7 Aug. 1964.

iest. It appears that the healthier the root stock, the longer it can continue to maintain new unoccupied shoots, and the more likely it will be that the new shoots will have ample thorns, Beltian bodies and foliar nectaries to provide a founding queen with the food and thorns necessary to rear her first brood rapidly.

There was no indication in this study that the young colonies moved around in the plot until they found the tallest shoots. Queen-units appear to be very stable in respect to staying with the original queen-shoot. Shoot abandonment and recolonization is associated almost entirely with auxiliary-units except when the shoots have been cut. The number of tall shoots, in areas such as plot KA, that lack old invader colonies matches very closely the number of new young colonies and new auxiliary-units.

The situation described above in plot KA was approximately replicated in treatment subplot H-2. In this subplot, the thorns of the unoccupied sucker shoots from the cut stumps were not clipped. By about the beginning of the rainy season, 30 young colonies had developed in situ on these stumps. The effect on the morphology of the shoot was striking. The top of each stump was enclosed in a cluster of nearly dead and badly stunted short branches that had been produced before the beginning of the rainy season. Out of the center of the cluster of branches there was usually a single well developed branch with intact leaves and shoot tip (Fig. 62). This branch was 30-100 cm long by 5 Aug. and was patrolled by 20-75 small workers from each of the young colonies. Those acacias that did not have new colonies in them did not show this new growth. Two of the shoots in this subplot were invaded by an auxiliary-unit from a large colony in control subplot H-3 about the middle of June. These two shoots developed in the same manner as those with young colonies in them.

Auxiliary-shoot effects. Among the emergent occupied shoots of *A. cornigera* in a single stand, there is often strong variation in the heights of the shoots. A major portion of this variation appears to be associated with various biotic factors in the environment rather than inherent physiological differences in growth rate. The sporadic damage of the rutelline scarab *Pelidnota punctulata* causes great variation in height as well as variation in life form; when it feeds on a shoot, it usually eats all of the undamaged shoot tips, and it is therefore several weeks or more before a positive height increment occurs. Since the incidence of feeding damage by *Coxina hadenoides* is influenced by the size of the colony on the shoot, height variation is also in part associated with the size of the colony.

In addition to the direct action of *Pelidnota punctulata* and *Coxina hadenoides,* the auxiliary-shoot phenomenon has a strong effect on height variation. What appears to happen in many cases is that a single colony occupies a shoot as a queen-shoot. This shoot grows vigorously and the colony likewise grows. As the colony becomes larger, it moves out to neighboring small and unoccupied shoots. When they become occupied, they have a positive height increment. As the rainy season progresses and the colonies grow, they incorporate more and more shoots into their individual groups of auxiliary-shoots. Since each successively occupied shoot started its vigorous upward growth later in the year, there is great variation in the individual heights of the shoots.

The auxiliary shoot effect was particularly noticeable in plots N, O, P, L, and M. These were plots with moderate shoot density, in which the original sizes of the colonies were relatively small, due to the fact that they were young colonies developed in situ or had their numbers severely reduced when the vegetation was last cut.

When the dry season starts in those areas that have high shoot density, and the new leaf production rate is lowered, there is a gradual abandonment of 10-50 percent of the auxiliary-shoots. By the end of the dry season, a much larger proportion of the occupied shoots are queen-shoots than is the case at the beginning of the dry season. When the rainy season begins, and colony expansion (both in size and area) begins again, the same progressive development of height increment began. As shoots become occupied by auxiliary-units, and as the auxiliary-units grow in size, the height increment rate of the shoots correspondingly increases. This took place in plots U and V.

Where the shoots are very close together over a large area, the acacias are not as free of insect damage as is expected. This is apparently due to the fact that in such a case, many of the shoots (as high as 50) have contacting branches. Due to the aggressiveness of a colony of *P. ferruginea,* this series of contacting shoots has to be occupied by one colony. However, it is not often that one colony is large enough to occupy effectively such a large series of shoots. Therefore, there is a higher incidence of insect damage than would occur if a colony of equal size was isolated in only 5-10 shoots.

Reproductive biology. As is the case with most of the woody plants growing in the experimental plots, *A. cornigera* reproduces both by seed and by suckers from root stocks. However, it does not possess the inherent physiological and morphological properties which are apparently responsible for the relative freedom from insect attack that is enjoyed by the majority of plant species in the area. The trait which insures freedom from serious insect damage, namely the occupation by a colony of *P. ferruginea,* is a trait which has to be acquired through development of a colony in situ, or invasion by a queen-unit.

The age at which a shoot becomes occupied is of utmost importance. Observations of seedlings on newly cleared sites show that the shoots rarely grow over 25 cm tall, or produce more than five swollen thorns and 25 leaves during their first rainy season and the following dry season. During this year of growth, in about half of the shoots that live to be a year old, at least one queen develops a colony with 10-50 workers in it. If the newly occupied seedling is growing at a site where it receives at least some direct sunlight, it grows upward to become a canopy member or emergent. If the seedling is not occupied by the beginning of the second rainy season, it is usually unable to grow more than another 10-20 cm until it becomes occupied. However, the longer it remains unoccupied, the higher is the probability that it will become too heavily shaded for growth, or will be eaten during the dry season by a rodent such as *Sigmodon hispidus*. Observations of seedlings of known age indicate that unoccupied seedlings rarely live more than two years after germination. On the other hand, young shoots that become occupied in sufficient time for them to become canopy members or emergents, generally live for 8-10 years in ungrazed regeneration. They set their first heavy seed crop at the end of the fifth dry season after the seeds germinate.

The suckers from stumps are generally faster than seedlings in developing a colony and becoming a canopy member or emergent. At the outset, these shoots have a swollen thorn at nearly every node, large numbers of Beltian bodies on the leaves, and functional nectaries on the petiole. They often grow to 30-50 cm in height while unoccupied. However, as with seedlings, there is still moderate to high mortality among unoccupied sucker shoots. While it is usually a year or more before a colony develops in a seedling, a colony with 10-100 workers is usually present in a sucker in less than nine months. Those suckers which are occupied at the beginning of their second rainy season grow vigorously, become canopy members or emergents, and live for 8-10 years. They set their first heavy seed crop at the end of the fourth dry season after the original shoot was cut or burned.

Frequently, in both natural and man-made disturbance sites, a colony does not develop in situ in suckers from stumps; the mature colony moves directly from the dead shoot into the new suckers. The shoot is occupied from the first day of growth. These shoots suffer almost no mortality during their first five years of growth. The first heavy seed crop is produced at the end of the third dry season after the original shoot was cut or scorched.

The age attained by a shoot is in part a function of the type of plant community. The figure of 8-10 years cited above is in reference to shoots growing in ungrazed regeneration. In old established pastures in the vicinity of Campo Cotaxtla, occupied shoots are commonly found with 10-15 annual rings; these shoots are growing in open grassland and are rarely over 5 m tall. On river banks and in old roadside drainage ditches throughout the study area, shoots of this age were occasionally encountered. In the area around Temascal the shoots in pastures and fallow corn fields rarely live over 5 years because of the sporadic cutting and burning of these sites.

The physiognomy of the vegetation at the time a seedling or sucker appears is also of importance. Seedlings and suckers in heavy shade usually die within 2-3 years, irrespective of the presence of a colony of *P. ferruginea*. A seedling or sucker growing on a site which is cleared but not burned, is in much greater danger of being shaded before it becomes occupied than a seedling or sucker on a site that has been burned. During the first year after a fire, the vegetation is much more irregular and lower than the regeneration following a cutting. Seedlings and suckers in brushy pastures are in less danger of being shaded than those in ungrazed vegetation; the cattle eat most of the vines and open the general canopy with their trails and browsing. The cattle generally ignore the young unoccupied *A. cornigera.*

The reproductive features described above are further complicated by the time of year at which the seed germinates, or the sucker shoots appear. Seeds usually germinate during the first two months of the rainy season, and are almost immediately in danger of being heavily shaded. During the dry season, the vegetation opens up somewhat, and allows sunlight to reach the lower strata. If the seedlings survive until this time, they are still very likely to be eaten by *Sigmodon hispidus,* and to have any new shoot tips eaten by the larvae of the gelichiid moth *Aristotelia corallina.* If the seeds germinate late in the rainy season, the seedlings generally do not grow a root system deep enough to be able to survive the drying of the upper layers of soil during the dry season.

If a shoot is cut or burned during the rainy season, the suckers are subjected to severe defoliation by the abundant insects. The new branches from the stumps are often stripped of all green vegetation, and at times, all of the green thorns are eaten; in such a case, a new colony cannot possibly develop in situ. By the time that insect populations are lowered by the cool and dry season, the root stock is often either dead or so weakened that it produces very few leaves and swollen thorns. If a shoot is cut or burned during the dry season, the new suckers are often vigorous and relatively free from insect damage. However, if such a shoot does not become occupied by the beginning of the following rainy season, the high height increment rate and condition value are abruptly lowered as the shoot is subjected to severe defoliation by insects.

Of the approximately 60,000 seeds that are produced by a shoot of *A. cornigera* in its lifetime in the Temascal area, somewhat less than one percent have the opportunity to be dispersed to sites for germination. The other 99 percent are destroyed by bruchids while in the legumes hanging on the shoots. Under natural conditions, dispersal by water and birds is further complicated by the relative paucity of newly created disturbance sites in which the new seedling can grow well. Dispersal to these sites is, however, aided by the habitat preferences of the birds concerned (newly disturbed sites) and the usual deposition site of the floating legumes (areas cleared by the action of the current). In areas of man's activities, there are usually many acres of recently disturbed vegetation within a very short distance of the seed-bearing shoot. In this case, birds are quite effective in distributing seeds to suitable areas. Furthermore, in the soil under any old stand of regeneration, there is undoubtedly a reservoir of viable seeds that have not germinated. Such seeds remain viable at least three years, and probably much longer.

Reproduction by seed is complicated by another factor. In man-made disturbance sites, the regeneration is frequently cut or burned when 1-5 years old. The shorter the time required for a shoot to produce its first heavy seed crop (about 22,000 seeds), the higher the probability that it will be able to set seed before it is killed. As was stated above, seedlings require five years, suckers with a colony developed in situ require four years, and suckers with a mature colony from the start require three years, to produce the first heavy seed crop. It is of importance to the shoot that the root system be able to continue to grow new shoots after each cutting and/or burning until a shoot is left long enough to set a seed crop. It should be remembered that the shoot has to survive at least nine months after the first heavy flower crop in order for the seeds to mature. It is likewise of importance that the ant colony is able to continue to move from the cut or scorched shoots into the new sucker shoots, rather than dying with the shoot. The habit of establishing auxiliary-units in neighboring unoccupied shoots is beneficial in that one mature colony can insure normal growth for more than one shoot. However, if the shoot density becomes so great that there is too much shoot surface area to patrol effectively, the growth rates of all of the shoots except the queen-shoot will be reduced. In natural disturbance sites, these factors are perhaps of slightly less importance since the vegetation is less frequently removed from these sites, and the shoots are more highly dispersed.

Naturally unoccupied shoots. The naturally unoccupied shoots in the study area can be roughly arranged into three groups: 1) seedlings and young suckers in which colonies are developing in situ, or that are later invaded by auxiliary-units, 2) well developed shoots that are abandoned by auxiliary-units during the dry season, but are later re-occupied, and 3) well developed shoots that were never occupied. Members of all of these groups are found in both natural and man-made disturbance sites. The first two have been discussed in sufficient detail in previous sections; the shoots in these two groups almost invariably do not contribute to the sexual reproduction of *A. cornigera* unless they are occupied for the major portion of their life spans.

Well developed shoots that were never occupied are extremely rare in the study area. This is in part due to the great ability of founding queens and auxiliary-units to find unoccupied shoots. This makes it very difficult to determine on an observational basis how much damage would be received by *A. cornigera* if *P. ferruginea* were not present. However, the experimental plots, the observations of unoccupied seedlings and young suckers, and the observations of the very rare unoccupied well developed shoots, show that the damage is very substantial. In spite of this, there are exceptional micro-habitats in which unoccupied shoots can grow; the presence of these few shoots indicates that *A. cornigera* probably would not become extinct in the study area were *P. ferruginea* (and *P. nigrocincta*) to become abruptly extinct.

All of the well developed unoccupied shoots of *A. cornigera* found in this study were growing in relatively barren habitats. The shoot in figure 47 was growing on barren open ground at the base of the dam at Temascal; it had 17 legumes on it and had produced several flowers during the 1964 dry season. It had never been occupied by *P. ferruginea.* Near Tierra Blanca, Veracruz, an isolated single unoccupied shoot about 2 m tall was found growing on a large sewage outwash delta below a drainage culvert; during most of the dry season its uppermost growing point was undamaged. In Temascal, an unoccupied shoot about 150 cm tall was found growing in a garden; during the dry season and the first month of the rainy season it was free from phytophagous insect damage. On a large gravel bar in the Rio Tonto east of Temascal, a twisted and water-washed 2 m tall unoccupied shoot was found with four legumes and several flowers; it was apparently able to survive the rainy season floods. The first three shoots mentioned above were tenanted by a colony of *Pseudomyrmex gracilis mexicana.* They were growing in sites where there were no other *A. cornigera* within 200 m, and phytophagous insects were undoubtedly very low in numbers in the immediate area of these three shoots.

Unlike the obligate dependence association of *P. ferruginea* on a swollen-thorn acacia, *A. cornigera* is not totally dependent upon *P. ferruginea* to grow. Not only have a few unoccupied shoots been found that are well developed, but it is also possible that there are sufficiently barren habitats such that unoccupied shoots can produce a seed crop. It is impossible to determine by observation if there are members of the occupied portion of the population of *A. cornigera* that retain the chemical characteristics that keep other species of Mimosaceae in the Temascal area relatively free from insect damage. Certainly no such shoots were among the approximately 2500 unoccupied shoots in the experimental plots.

Economics. From conversations with land owners, and by observations of pastures, it was evident that in the study area, *A. cornigera* is an economic weed of some importance. On sites that are burned on a regular annual basis (permanent corn fields, cane fields, and some grass pastures), *A. cornigera* is present only as a very minor element of the vegetation; the few shoots are usually less than 50 cm tall, stunted, nearly dead, and unoccupied. On sites that are cut and/or burned on a relatively haphazard schedule, *A. cornigera* is often a common and vigorous plant. In brushy pastures it shares a dominant position with such woody plants as *Croton glabellus, Bixa orellana, Eupatorium odoratum, Parmentiera edulis, Bauhinia ungulata,* and *Jatropha urens;* none of these species are eaten by cattle. In well established grass pastures, *A. cornigera* occasionally comprises more than 90 per cent of the woody vegetation. At times it became so dense in patches that it is impossible to walk between the plants without being stuck by the thorns.

The production of dense vigorous stands of *A. cornigera* is primarily due to the way in which land is cleared. In both brushy and grass pastures, it is a common practice to cut the woody vegetation with a machete at intervals of 0.5-3 years; often this is not followed by burning. The cut shoots are left lying over the stumps and the old mature colonies move into the new sucker shoots. This cutting appears to cause almost no mortality among the root systems of *A. cornigera,* while it appears to gradually eliminate the other species of woody plants. In fact, when the shoots of *A. cornigera* are cut, the colonies often move in part into neighboring stunted shoots that were previously unoccupied; thus the ratio of occupied to unoccupied shoots is increased by this type of cutting. In some areas around La Granja, the practice of cutting without burning has been followed for at least 15 years with no decrease in the density of vigorous shoots of *A. cornigera.*

Cutting is occasionally followed by burning in brushy and grass pastures. Since the cut shoot with its ant colony is lying at ground level, it is consumed by the fire. This burning usually occurs during the dry season. During the following year it is necessary for a colony to develop in situ in the sucker shoots before the ant colony develops, but generally the root stock is strong enough to survive without a vigorous shoot until a colony is large enough to occupy the shoot. The critical factor in this type of shoot and colony destruction is that this burning does not occur every year. It appears that as long as the root system bears an occupied vigorous shoot for at least 1-2 years, it is then able to survive for the six months to a year following a fire while a colony develops in situ. It should be emphasized that in the pastures examined, it is insect damage that stunts the unoccupied suckers of *A. cornigera,* and not the browsing of cattle.

A further complication arises when newly cut brushy pastures are not burned evenly. It is often the case that the fires burn in strips and patches, and the cut shoots of *A. cornigera* are occasionally missed. If the unburned cut shoot contained a queen-unit, the colony then moves into an available sucker shoot. If it contains an auxiliary-unit, it also moves into a sucker shoot, but the unit gradually dies over a period of one to two months. However, the shoot is occupied during that period and often grows to a height of 50-100 cm above that of the unoccupied suckers in the pasture.

In grass pastures, the basal circle has to be taken into consideration. During the dry season, the grasses are often trampled and grazed to ground level by the cattle. If such a pasture is burned, the fire usually passes rapidly. As long as the shoots are not cut, the colony of *P. ferruginea* is often high enough so that the heat does not kill it. On some occasions, the lower trunk is not scorched due to the complete lack of imflammable materials in the basal circle. It should be emphasized that this is usually the case only in grass pastures where the dry grasses are lying very close to the ground. In taller vegetation, the trunk is usually scorched, but the ant colony often survives.

It appears that *A. cornigera* can be removed from pastures with relatively minor changes in management plans. In established corn and cane fields it is not present, or if present, is a very minor part of the vegetation; this appears to be almost entirely due to the annual burning of these fields. If pastures could be burned on an annual basis, the same effect would undoubtedly be achieved. However, regular annual burning is regarded by the land owners as detrimental to the soils, and to many of the grasses which are being promoted in the pastures. Since regular annual burning cannot be used, an equivalent practice should be effective. If the cut shoots are piled and burned, or just piled, 50 or more meters from any *A. cornigera* stumps, the new suckers from the cut stumps will be unoccupied. After this has been done annually for 2-4 years, it is very unlikely that *A. cornigera* will form more than a very minor part of the woody vegetation. There is the continuous threat of new colonies developing in situ in seedlings, but as larger and larger areas are cleared of their vigorous stands of *A. cornigera,* the frequency of both seedlings and founding queens will be greatly reduced.

DISCUSSION

At both the individual and population level, *Acacia cornigera* has characteristics which are associated with its interaction with *Pseudomyrmex ferruginea.* These characteristics fall into two groups. The less controversial characteristics are those which are necessary for the maintenance of a colony of the ant: swollen thorns, Beltian bodies, and foliar nectaries. These features are discussed at length in the first section of this paper. In view of the interdependent relationship that has been demonstrated between the ant and the acacia, it is certain that the present-day selective pressure, which makes the energy expended in the production of these three morphological structures profitable to the acacia, is the phytophagous insect damage with subsequent shading that is experienced by the acacia when it is not occupied by *P. ferruginea* (or *P. nigrocincta*). The characteristics that require close observation under experimental conditions for verification, are ecological and physiological, and the shoot requires occupation by *P. ferruginea* for their normal expression. In this latter group are the acacia's (1) high growth rate, (2) relative freedom from insect and mamal damage, (3) freedom from use by vines as a standard, (4) emergent or canopy member position, (5) abundance in man-made disturbance sites, and (6) attainment of sexual maturity. These interdependent points are discussed below.

Observations in both natural and man-made disturbance sites in the study area show that *A. cornigera* has a height increment rate which is superior to that of most woody plants during the first 8-12 years of secondary succession. This is evidenced by its position as a canopy member or emergent, and by the recorded rate of main-axis elongation of 2.50 cm per 24-hour day. However, in the experimental plots, it is clearly shown that if the colony of *P. ferruginea* is removed from the shoot, this high height increment rate is abruptly lowered. This is likewise the case for the high rate of leaf and thorn production, excellent condition of the shoot, and high total biomass production. In the experimental plots, this reduction is a result of the feeding activities of phytophagous insects and rodents, which are normally prevented by *P. ferruginea* from feeding on the shoot. In addition, once the unoccupied shoot looses its ability to keep up with the surrounding vegetation, it becomes shaded, and this further stunts its growth. There is no doubt that this reduction in growth is due to these factors, rather than to some detrimental effect of the techniques used to remove the ants in the treatment subplots. In addition to damage of the unoccupied shoots, there is high mortality of the shoots due to the cumulative effect of shading and repeated damage. The slowing of growth rates, and direct mortality through the damage of unoccupied shoots, is of obvious significance in natural selection for shoots with the properties necessary to maintain a large colony of *P. ferruginea* (swollen thorns, Beltian bodies, nectaries).

The differences in growth rate and mortality between occupied and unoccupied shoots are of course affected by some major variables: the time of year, the structure of the plant community, and the sizes of the occupant ant colony. During the dry season, growth rates of all the plants in the community are reduced or stopped. Associated with this, there is a great lowering of phytophagous insect activity. However, growth rates of *A. cornigera* are only partly lowered; continued leaf production and maintenance during the dry season are necessary for survival of the ant colony. But since phytophagous insect activity is greatly lowered and the shade of the general surrounding vegetation is greatly reduced, unoccupied shoots are able to grow more at this time of year than at any other. This factor makes the natural abandonment of some shoots by auxiliary-units during the dry season of much less serious consequence than abandonment during the rainy season (a very rare occurrence). It should be noted that this abandonment occurs as a consequence of partial or total failure of the shoot to produce sufficient food for the unit of ants. However, as long as sufficient shoots are present in the acacia population with nectaries and new leaves with Beltian bodies, to support the colonies present in a given area, abandonment during the dry season is of little immediate consequence to *P. ferruginea.* Thus, certain variation in reaction to the dry season by leaf drop and growth cessation within the population of *A. cornigera,* where dense, is not inimical to the existence of the ant-acacia interaction; when the rainy season begins, the ants move back into the abandoned shoots. Since phytophagous insect activity increases greatly during the rainy season, unoccupied shoots have almost no growth, while the occupied shoots grow vigorously. It should be remembered that in those areas where *A. cornigera* has a low population density, it is less likely that there will be a nearby shoot with food for a starving colony to move into if it abandons its unproductive shoot. In this case, there should be severe selection for shoots with the ability to continue to produce food for the ant colony throughout the dry season. Relatively low densities of *A. cornigera* are the rule in natural disturbance sites.

While the structure of the plant community has a relatively small effect on the quantity of phytophagous insect damage (it is nearly always severe), it has a large effect on the degree of shading of shoots, and consequent shoot mortality. In the dense vegetation of ungrazed secondary succession, unoccupied shoots quickly become heavily shaded due to their inability to keep above the rising vegetation, that is in turn due to the lowered growth rate. Even if a shoot becomes occupied while it is heavily shaded, it is normally unable to reach the canopy and become sexually reproductive. However, in heavily grazed and browsed pastures, many of the shading shrubs and vines are thinned out; the insolated unoccupied shoots produce more leaves and swollen thorns and appear to be more tolerant of insect damage. Due to this, a colony of *P. ferruginea* has a longer time to develop in situ before the shoot is killed by cumulative insect or rodent damage. In this sense, it can be said that cattle promote the survival of unoccupied acacias. Grazing and browsing likewise reduce the selective pressure against shoots which are slow to acquire an ant colony, or have low height increment rates. Those very few shoots which reach sexual maturity without being occupied by *P. ferruginea* are virtually always growing on sites that have been almost completely cleaned of other vegetation (e.g., rock quarries), or for some other reason have very low phytophagous insect populations.

Even though the shoot is occupied by a queen-unit or auxiliary-unit of *P. ferruginea,* it is of course not guaranteed to have a high growth rate. The larger the unit in proportion to the size of the shoot, the less insect damage and shading occurs. In view of this, it is expected that there is strong selection for shoot characteristics that promote the rapid growth of the colony—such as heavy nectar flow, high and continuous rate of Beltian body production, large and durable swollen thorns, and the growth of new suckers from cut stumps with the foliar characteristics of a mature shoot. Not only does the colony need to be large for efficient patrolling of the shoot, but the weather conditions must be suitable for normal worker activity outside of the thorn. *P. ferruginea* has developed the ability to be active under much more inclement weather than those *Pseudomyrmex* not associated with living plants. Associated with this, it is not surprising that *P. ferruginea* has developed the behavioral trait of being active outside of the thorns throughout the 24-hour day (Fig. 32 and 33), quite in contrast to those species of *Pseudomyrmex* which are not obligatorily associated with living plants. These latter are strictly diurnal in their foraging behavior. It should be noted that variation in the size of the ant colony and in weather conditions, were the two factors of most importance in the promotion of variation in height increment rate and condition of *A. cornigera* in the experimental plots.

Like the surrounding vegetation in the plant community, heavily occupied shoots of *A. cornigera* show little obvious insect damage to the leaves and shoot tips. It should be noted however, that upon close examination most species of plants in the plant community demonstrate minor to major damage to growing points that is not immediately obvious. Further, damaged plant parts are not always obvious because they have been removed by the insect. This is of course not the case with unoccupied shoots of *A. cornigera*. Naturally unoccupied shoots, such as very young suckers and seedlings, have a very high frequency of shoot tip destruction and their mature leaves are usually badly damaged. This damage is however, normal for the reproductive biology of *A. cornigera,* and some of these plants survive until they become occupied. It is noteworthy that young unoccupied shoots of *A. cornigera* are able to live for periods of 1-2 years with only 4-10 mature leaves; there is not, however, any evidence that seedlings or young suckers are any less palatable to phytophagous insects than mature shoots. In the experimental plots, it has been clearly shown that the frequency of insect damage is greatly increased if the ant colony is removed (Tab. 15-27). This removal of the ants results in a great lowering of growth rate (Tab. 4-13) by removal of the shoot tips by phytophagous insects. However, as the mature leaves are destroyed, and more and more shoot tips are eaten, the plant is weakened and its physiological ability to have a high production rate is lowered as well. It is probable that in this weakened state, the shoot is much more susceptible to attacks by the wood-boring buprestid larvae of *Chrysobothris* sp. near *C. multistigmosa.* In addition, if the branches are cut off of such weakened shoots, the stump shows very poor production of new foliage. It should be remembered that the direct consequence of failure to grow, shading by the rising surrounding vegetation results in lowering of the physiological growth rate as well.

With the exception of those insects that have developed the ability to withstand or avoid the attack of *P. ferruginea,* occupied shoots are virtually free of phytophagous insects. This has been shown quite clearly by the censuses of insects on occupied and unoccupied shoots (Tab. 1). That this difference is due to the activity of the ants, and not some property of the shoots, is shown by the several hundred observations in this study of these same species of insects being attacked and removed from the shoot by the ants. Thus, while it is obvious that plants have many characteristics that allow only those insects adapted to those characteristics to feed on them, it appears that *A. cornigera* has lost some of these characteristics (bitter chemicals in the new foliage, fibrous tissues in new foliage, canopy member or submergent). However, in return it has gained a characteristic that serves the same purpose, namely *P.*

ferruginea. Occupation by the ant requires an expenditure of energy on the part of the shoot in the form of swollen thorns, Beltian bodies, foliar nectaries, and new leaves during the dry season. In return, the shoot is effectively relieved from the phytophagous insect damage which was shown by this study to be inflicted on unoccupied shoots. *A. cornigera* (and other swollen-thorn acacias) is unique among plants in that one of its major deterrent characteristics to insect attack can be experimentally removed without directly altering the morphology or physiology of the plant. Associated with this, the new seedling or sucker does not inherently possess the characteristic that allows *A. cornigera* relative freedom from insect attack; a colony of *P. ferruginea* must develop in situ or invade from another shoot.

Unfortunately, the role that *P. ferruginea* plays in deterring mammals could not be thoroughly documented. In this study, occupied shoots showed almost no mammal damage. There is little doubt that the rodent *Sigmodon hispidus* is deterred by *P. ferruginea* from eating young shoots if the shoots are occupied. At present, cattle are the only large browsing mammals that are abundant enough to detrimentally affect *A. cornigera.* In view of the willingness of the Brocket Deer to eat *A. cornigera* foliage, and the active browsing of cut shoots by cattle, the reluctance of cattle to browse standing *A. cornigera* in their pastures is probably not due to a bad taste in the plant foliage. Likewise, the thorns do not have an absolute deterrent effect on either the Brocket Deer or cattle. In fact, they did not appear to have any effect on the feeding of these two mammals. However, it is reasonable to expect that the thorns might cause the plant to be placed somewhat lower on the host plant preference list of large browsing mammals. In view of the Brocket Deer's reaction to *P. ferruginea,* it is likely that under natural circumstances it would not feed on occupied shoots. As far as cattle are concerned, it is still only indirect evidence that indicates that they are turned away from occupied shoots by the ants, but it is difficult to imagine for what other reason they do not browse *A. cornigera* freely.

As is the case with most plants, there are a few insects that have evolved to feed on *A. cornigera* despite its characteristics. These are the few insects that are not efficiently removed by the ants, such as *Pelidnota punctulata, Coxina hadenoides, Syssphinx mexicana, Rosema dentifera, Acanthoscelides oblongoguttatus, Mimosestes* sp. However, *A. cornigera* shows good growth in spite of the damage by these insects. These insects may be regarded in the same light as other insects in the environment which, though they feed on their host plants, have evolved to a state of balance whereby they do not destroy their host population, yet they harvest enough of it to survive. There are a few insects such as *Mozena tomentosa* and *Aristotelia corallina* that normally are found only on naturally unoccupied shoots; they are in large part responsible for the very slow growth rate of unoccupied young suckers and seedlings. No one of the eight species listed above, nor the cumulative sum of their feeding, is serious in comparison to the sum effect of those insects that feed on the plant when the ants are removed.

It must be noted that a major part of the usefulness of *P. ferruginea* to *A. cornigera* depends on the presence of phytophagous insects in the environment that will feed on *A. cornigera* when the ants are removed. In the Temascal area, there are at least 40 species of insects that feed on unoccupied shoots of *A. cornigera*. While each individual insect does relatively little damage in comparison to that done by an individual of an insect such as *Pelidnota punctulata,* the cumulative effect of these insects feeding on the shoots night and day, and in relatively large numbers, is almost entirely responsible for the lack of growth and poor condition of unoccupied shoots in the experimental plots. As one would expect, the normal primary host plants of these insects are the numerous species in mimosaceous genera that occur in the same plant community with *A. cornigera,* e.g., *Calliandra houstoniana, Leucanea glauca, Acacia farnesiana, Acacia macracantha, Acacia angustatissima, Enterolobium cyclocarpum, Mimosa albida, Inga* sp., and others. Each of these plant species has a number of insect species that feed heavily on it, and occasionally on other plants. In other words, the insects which feed on unoccupied *A. cornigera* have host preference lists, at the top of which is some other species of plant (often a mimosaceous genus) and at the bottom of the list is occupied *A. cornigera.* Removal of the ants moves *A. cornigera* very close to the tip of the host preference list.

It is clear from the experimental plots, observation of naturally unoccupied shoots, and the reaction of workers of *P. ferruginea* to foreign vegetation, that the ant prevents vines and lateral branches from growing into the canopy of occupied *A. cornigera.* Structurally, an occupied shoot is ideal for the support of vines. It has a stiff and often emergent central axis with strong lateral branches extending out into, and over, the general canopy. The numerous swollen thorns are excellent sites for tendril attachment. However, occupied shoots are almost invariably free of living vines due to the ant's habit of mauling foreign vegetation. It should be noted that the other emergent woody plants in the first several years of succession have structural properties which lower the frequency of vines using them for standards (e.g., *Bixa orellana, Croton glabellus, Bauhinia ungulata*). These plants have slightly drooping leaves with long petioles and very smooth upper surfaces; as they blow in the wind, it is very difficult for vine runners to become attached to them. They also have very smooth bark. In addition, these plants do not develop many lateral branches, and this removes another potential vine support. Associated with this, many of the vines that use unoccupied shoots of *A. cornigera* as standards normally have their primary growth in a lateral direction through the general canopy rather than piling up on the emergent species of plants.

When a canopy member, or emergent, shoot of *A. cornigera* is deprived of its ant colony in ungrazed vegetation, the vines frequently form a heavy mat over the shoot, or use it as a standard to rise above the general canopy. The emergent unoccupied shoots often accumulate very heavy masses of vines during the rainy season, and as a consequence are bent over and firmly bound into the general canopy. However, the thing that makes the unoccupied shoot most severely susceptible to vine damage is that there is also such severe insect damage to the shoot tips that the shoot cannot grow up through the vine mat. Virtually all of the mature foliage present at the time the ants are removed becomes shaded by the vines. Thus not only does the ant alleviate the potential danger of the vines by mauling them, but it also is responsible for protecting the rapidly elongating main shoot tip which is the only protection against vines that the shoot could have were the ants to be removed.

As a vertical downward extension of the workers' activity in keeping foreign vegetation out of the canopy of *A. cornigera,* the workers often produce a bare basal circle under the shoot that is free of living foliate parts of other plants. If the workers gain directly from their chewing of vines in the canopy (i.e., by getting plant juices), they very likely profit in the same direct manner when mauling vegetation in the basal circle. However, it is more likely that the use of the basal circle to *P. ferruginea* is indirect. When the basal circle is large, fires passing through the general vegetation during the dry season are less likely to destroy the ant colony. This is of great significance to *A. cornigera* in that while the shoot is often killed by fire, suckers from the roots are immediately occupied by the mature ant colony. In addition it is likely that the bare basal circle lowers the incidence of phytophagous insects reaching the shoot. The removal of foreign vegetation from the canopy of *A. cornigera* may serve the same purpose.

In view of the definite effect that *P. ferruginea* has on the growth rate of shoots of *A. cornigera,* it is reasonable to consider the ant-acacia interaction in explaining the abundance of *A. cornigera* in man made disturbance sites in contrast to other species of acacia. In the area between Temascal and La Granja, there are at least five native species of acacia: *A. cornigera, A. macracantha, A, chiapensis, A. farnesiana,* and *A. angustatissima.* All of these species grow in natural disturbance sites such as river banks and arroyos; while *A. cornigera* is often the most common, none of the species have an outstanding dominance in respect to numbers of individuals. While all five species have invaded man's fields and pastures, only *A. cornigera* has become widespread and very abundant. In some fields and pastures, it is an economic weed of considerable importance. Initially, this successful population expansion was due to the efficient dispersal of seeds by birds both to the newly cleared sites, and between areas under continuous disturbance. The seeds of the other four species of acacia are distributed by gravity and water. Once a plant of *A. cornigera* has become established, it grows rapidly, and is very hardy even when the shoot is repeatedly cut or burned. However, in the case of both of these factors (seed dispersal and shoot hardiness) *P. ferruginea* must be considered. Unoccupied shoots do not normally survive long enough to produce seeds which can then be dispersed. Secondly, even if the roots of an established plant produce new suckers after the shoot has been killed, an ant colony must be present to occupy the shoot, in order for successful growth to occur. Thus it is that fields that are annually burned lack *A. cornigera* as maturing shoots. Associated with this is the significant fact that the sooner a shoot becomes occupied, the sooner it produces its first heavy seed crop. This becomes very important in an area where the vegetation is cut frequently (on a 2-5 year cycle). Finally, it is very doubtful that *A. cornigera* would have become so common in man-made disturbance sites had *P. ferruginea* been unable to move out of the natural disturbance sites with it, and had *P. ferruginea* been unable to survive under the various shoot and colony destruction regimes that man's activities produce.

Based on the data presented and discussed above, the following conclusion appears justified. *Pseudomyrmex ferruginea* is dependent upon a swollen-thorn acacia for survival, and *Acacia cornigera* is dependent on an obligate acacia-ant for normal development; the interaction between the two can therefore be properly termed one of obligatory mutualism. Were all the colonies of *P. ferruginea* (and *P. nigrocincta*) in the study area to abruptly disappear, the density, distribution, and condition of the population of *A. cornigera* would be drastically lowered. Individual shoots would survive in relatively isolated sites, and under unusual circumstances. Presumably, the population would be able to evolve the characteristic resistance to insects and mammal damage that is displayed by the species of *Acacia* that are not associated with ants.

Thus, as was stated in the introduction, the opinions of earlier authors who felt that the ant "protects" the acacia have been clearly substantiated by this study. This does not apply of course to the other ant and plant relationships that these authors also discussed. The bearing of the demonstrated obligate mutualism between *P. ferruginea* and *A. cornigera* on other ant-plant interactions will be discussed in a later paper. However, it should be noted that interpretation of the facts associated with these other interactions is made much simpler by the present understanding of the interaction between *P. ferruginea* and *A. cornigera.*

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